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The Morphology of the Syrinx in Passerine Birds

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The Morphology of the Syrinx in Passerine Birds

Peter L. Ames

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THE MORPHOLOGY OF THE SYRINX IN PASSERINE BIRDS

PETER L. AMES

ABSTRACT

The syrinx, for more than a century an important organ in determining the subdivisions of the avian order Passeriformes (perching birds), was examined in 983 specimens, representing 65 of the 67 families recognized by most modern authorities. Particular emphasis was placed on the suborder Tyranni and especially on the family Tyrannidae (tyrant flycatchers).

The three general morphological categories established by Müller in 1847 form the basis for the major subdivisions now in use. Of Müller's divisions, two appear valid taxonomic units: the "Tracheophonae" (the modern superfamily Furnarioidea) and the "Polymyodae" (the suborder Passeres or oscines, often called songbirds). Müller's third category, the "Picarii," contains both simple and relatively complex syringeal types. Taxonomic decisions based on the simple type (in which intrinsic muscles and cartilaginous elaborations are lacking) should be made cautiously, since it apparently represents the ancestral "pico-passerine" syrinx. Certain results of this study suggest changes in the current classification of the Passeriformes.

1) The antbird-ovenbird complex, now usually considered a superfamily (Furnarioidea) in the suborder Tyranni, should be elevated to subordinal rank (Furnarii). This group is characterized by a highly specialized vocal apparatus that sets them apart from other passerines. There are, moreover, no other structural characters that ally this group to any other passerine group in particular.
   a) The Furnariidae (ovenbirds) are closest to the Dendrocolaptidae (woodcreepers), but may be separated from them by the absence (except in *Geositta*) of dorsal and ventral "horns" on the Processi vocales.
   b) The Formicariidae (antbirds) fall into two structural groups, based on several features of the syrinx, reinforced by external characters. These may be called "typical antbirds" (*Thamnophilus* and others) and "ground antbirds" (*Grallaria, Conopophaga* and others).
2) The Cotingidae (cotingas), as presently classified, include several syringeal types.
   a) *Attila, Casiornis, Rhytipterna* and *Laniocera* appear to be more closely related to the Tyrannidae, especially to *Myiarchus,* than to the more colorful cotingas, with which they are usually placed, but from which they differ in possessing oblique intrinsic muscles and internal cartilages. The becards (*Pachyramphus* and *Platypsaris*) also appear to belong with the Tyrannidae.
3) In the Tyrannidae (tyrant flycatchers) the syrinx is characterized by the presence of oblique intrinsic muscles and internal cartilages. There are several structural

groups, varying in homogeneity. In general, these groups support the classification of Hellmayr (1927).

a) *Sayornis* appears to be closer to *Empidonax* and *Nuttallornis* than to the *Fluvicola* group.

b) *Myiozetetes, Sirystes* and *Legatus* do not appear to belong in the middle of a linear series that includes *Muscivora, Tyrannus, Empidonomus, Myiodynastes, Megarhynchus, Pitangus* and *Tolmarchus.*

c) The subfamily Platyrinchinae, characterized by broad, flat bills, seems to be an artificial assemblage, if the wide differences in syringeal structure among the three genera (out of the five) studied are considered.

d) The genera *Terenotriccus, Pyrrhomyias, Myiobius* and *Onychorhynchus,* along with the manakin *Piprites,* form a group characterized by the absence of intrinsic muscles and (in most) by syringeal asymmetry.

4) The sharpbill (*Oxyruncus*) has the oblique intrinsic muscles and internal cartilages characteristic of the Tyrannidae, but the details of the syrinx are not of much help in determining to which group of tyrant flycatchers the sharpbill is closest.

5) Three small Old World families, the Pittidae, Philepittidae and Acanthisittidae, currently placed in the suborder Tyranni entirely on the basis of their syringeal structure, show no obvious relationship to any New World families. The syrinx of the Philepittidae is remarkably like that in the broadbills *Psarisomus* and *Serilophus,* with which *Philepitta* shares certain features of the sternum and pterylosis. The Philepittidae may well be more closely related to the Eurylaimidae than to the Tyranni or the Furnarii.

6) The scrub-birds (Atrichornithidae) are more like the lyrebirds (Menuridae) in syringeal structure than previously believed. Both have three pairs of intrinsic muscles, arranged in a pattern much like that found in songbirds (Passeres).

7) The suborder Passeres has been extensively studied. It is far less variable in syringeal structure than the Tyranni or Furnarii. The syrinx is complex but uniform throughout the suborder, suggesting that the group is narrowly monophyletic. The absence of the pessulus in the larks (Alaudidae) should not be considered primitive, for its absence is almost certainly secondary. The pessulus is present in most suboscines and in the nonpasserine orders Piciformes and Coraciiformes, and was probably present in the ancestor of the Passeres.

ZUSAMMENFASSUNG

Die Syrinx, seit mehr als einem Jahrhundert dazu benutzt, die Gattungen der Passeriformes (Sperlingsvögel) von einander abzugrenzen, wurde bei 983 Exemplaren untersucht, Material, das sich auf 65 der 67 von den meisten modernen Sachverständigen anerkannten Familien verteilt. Besondere Aufmerksamkeit wurde der Unterordnung der Tyranni zugewandt, hauptsächlich der Familie der Tyrannidae.

Die drei von Müller 1847 aufgestellten Kategorien bilden die Grundlage für die Hauptunterteilungen, die jetzt gebräuchlich sind. Von Müller's Gruppen scheinen zwei

wohlbegründete taxonome Einheiten zu sein: die "Tracheophonae" (die moderne Superfamilie der Furnarioidea) und die "Polymyodae" (die Unterordnung der Passeres oder Oscines, oft Singvögel genannt). Müller's dritte Einheit, die "Picarii", enthält sowohl einfache als auch relativ komplizierte Syrinx-Typen. Taxonomische Entscheidungen, die auf dem einfachen Typus (bei dem "intrinsische" Muskeln und knorpelige Bereicherungen fehlen) begründet sind, sollten mit Vorsicht gehandhabt werden, da dieser Typ anscheinend die ursprüngliche "pico-passerine" Syrinx darstellt. Bestimmte Ergebnisse dieser Untersuchung legen Anderungen in der gegenwärtigen Einteilung der Passeriformes nahe.

1) Der Ameisenvögel-Töpfervögel-Komplex, der zur Zeit gewöhnlich als eine Superfamilie (Furnarioidea) in der Unterordnung der Tyranni betrachtet wird, sollte in den Rang einer Unterordnung (Furnarii) erhoben werden. Diese Gruppe wird charakterisiert durch einen sehr spezialisierten Stimmapparat, der sie von den anderen Passerinen unterscheidet. Ausserdem gibt es keine anderen Strukturmerkmale, die diese Gruppe mit irgendeiner anderen Sperlingsvögel-Gruppe besonders verbindet.
   a) Die Furnariidae (Töpfervögel) stehen den Dendrocolaptidae (Baumsteiger) am nächsten, können aber von ihnen getrennt werden durch das Fehlen von dorsalen und ventralen "Hörnern" der Processi vocales (ausgenommen *Geositta*).
   b) Die Formicariidae (Ameisenvögel) zerfallen hinsichtlich mehrerer Merkmale ihrer Syrinx in zwei Gruppen, was äussere Kennzeichen bekräftigen. Sie können als "typische" Ameisenvögel (*Thamnophilus* und andere) und "Boden"-Ameisenvögel (*Grallaria, Conopophaga* und andere) bezeichnet werden.
2) Die Cotingidae (Kotingas) wie sie zur Zeit zusammengefasst werden, weisen mehrere Syrinx-Typen auf.
   a) *Attila, Casiornis, Rhytipterna* und *Laniocera* scheinen mit den Tyrannidae, besonders mit *Myiarchus,* näher verwandt zu sein als mit den farbigeren Formen, mit denen sie gewöhnlich zusammengestellt werden, von denen sie sich aber unterscheiden indem ihnen schräge, "intrinsische" Muskeln und innere Knorpel eigen sind. Die *Pachyramphus-* und *Platypsaris*-Arten scheinen auch zu den Tyrannen zu gehören.
3) Bei den Tyrannidae wird die Syrinx gekennzeichnet durch das Vorhandensein von schrägen, "intrinsischen" Muskeln und inneren Knorpeln. Es gibt mehrere Struktur-Gruppen, die in ihrer Gleichartigkeit variieren. Im allgemeinen bestätigen diese Gruppen die Einteilung von Hellmayr (1927).
   a) *Sayornis* scheint *Empidonax* und *Nuttallornis* näher zu stehen als der *Fluvicola*-Gruppe.
   b) *Myiozetetes, Sirystes* und *Legatus* scheinen nicht in die Mitte der gradlinigen Reihenfolge zu gehören, die *Muscivora, Tyrannus, Empidonomus, Myiodynastes, Megarhynchus, Pitangus* und *Tolmarchus* einschliesst.
   c) Die Unterfamilie Platyrinchinae, die durch breite, flache Schnäbel gekennzeichnet wird, scheint eine künstliche Gruppe zu sein, wenn man die grossen Unterschiede in der Struktur der Syrinx zwischen den drei (von fünf) Gattungen, die untereucht wurden, bedenkt.
   d) Die Gattungen *Terenotriccus, Pyrrhomyias, Myiobius* und *Onychorhynchus* zusammen mit der Pipride *Piprites,* bilden eine Gruppe, die durch das Fehlen

von "intrinsischen" Muskeln und (in den meisten Fällen) durch das Vorhandensein von Asymmetrie der Syrinx gekennzeichnet wird.

4) Der Flammenkopf (*Oxyruncus*) hat die schrägen, "intrinsischen" Muskeln und die inneren Knorpel, die die Tyrannidae kennzeichnen, indessen tragen die Einzelheiten des Syrinxbaues wenig dazu bei um zu bestimmen, welcher Gruppe der Tyrannen er am nächsten steht.

5) Drei kleine Familien der Alten Welt, die Pittidae, Philepittidae und Acanthisittidae, die zur Zeit lediglich auf Grund der Struktur ihrer Syrinx in der Unterordnung der Tyranni eingeordnet werden, zeigen zu keiner der neuweltlichen Familien eine offensichtliche Verwandtschaft. Die Syrinx der Philepittidae ist auffallend ähnlich derjenigen der Eurylaemiden *Psarisomus* und *Serilophus,* mit denen sie bestimmte Merkmale des Brustbeines und der Pterylose teilen. Die Philepittidae dürften wohl näher mit den Eurylaimidae verwandt sein als mit den Tyranni oder den Furnarii.

6) Die Atrichornithidae sind in der Struktur ihrer Syrinx den Leierschwänzen (Menuridae) ähnlicher, als man bisher geglaubt hat. Beide haben drei Paare "intrinsischer" Muskeln, die in einer Weise angeordnet sind, die derjenigen der Singvögel (Passeres) sehr ähnlich ist.

7) Die Unterordnung der Passeres wurde eingehend untersucht. Sie ist in der Struktur ihrer Syrinx weit weniger variabel als die Tyranni oder die Furnarii. Die Syrinx ist kompliziert, aber in der Unterordnung überall einheitlich, was nahelegt, dass die Gruppe streng monophyletisch ist. Das Fehlen des pessulus bei den Lerchen (Alaudidae) sollte nicht als primitiv angesehen werden, da dieser Mangel sekundär sein dürfte. Der pessulus ist bei den meisten Suboscines und bei den nicht-passeriformen Ordnungen der Piciformes und Coraciiformes vorhanden und war wahrscheinlich auch bei den Vorfahren der Passeres ausgebildet.

RESUMEN

La siringe, utilizada por más de un siglo como órgano importante para determinar las subdivisiones del orden Passeriformes (pájaros), fué examinada en 983 ejemplares, representando 65 de las 67 familias reconocidas por la mayoría de las autoridades modernas. Se puso atención especial en el suborden Tyranni y sobretodo en la familia Tyrannidae (atrapamoscas tiranas).

Las tres categorías generales morfológicas establecidas por Müller en 1847 forman la base de las subdivisiones más importantes ahora en uso. De las divisiones de Müller, dos de ellas parecen ser unidades taxonómicas válidas: las "Tracheophonae" (la superfamilia moderna Furnarioidea) y las "Polymyodae" (el suborden Passeres u oscines, frecuentemente llamados pájaros canoros). En la tercera categoría de Müller, los "Picarii", se encuentran siringes de forma sencilla así como otras de forma compleja. Decisiones taxonómicas basadas en el tipo sencillo (en el cual los músculos intrínsecos y las elaboraciones cartiloginosas no existen) deben ser hechas cautamente, porque aparentemente este tipo representa la siringe "pico-paserino" ancestral. Algunos resultados de este estudio sugieren cambios en la clasificación actual de los Passeriformes.

1) El grupo hormiguero-hornero, considerado usualmente hoy en día como una superfamilia (Furnarioidea) en el suborden Tyranni, debe ser elevado a la categoría de suborden (Furnarii). Este grupo se caracteriza por poseer un aparato vocal altamente especializado que lo distingue de los otros grupos paserinos. Además, no tiene ninguna otra característica estructural que lo una con ningún otro grupo paserino en particular.
   a) Las Furnariidae (horneros) tienen sus nexos mas cercanos con las Dendrocolaptidae (trepadores). Se distinguen de éstas por la ausencia (excepto en *Geositta*) de eminencias corniformes dorsales y ventrales en los Processi vocales.
   b) Las Formicariidae (hormigueros) pueden divisarse in dos grupos estructurales basados en algunas características de la siringe que muestran cierto paralelismo con algunos caracteres externos. Estos pueden llamarse "hormigueros típicos" (*Thamnophilus* y otros) y "hormigueros terricolas" (*Grallaria, Conopophaga* y otros).
2) Las Cotingidae (cotingas), como son clasificadas actualmente, contienen varios tipos de siringe.
   a) *Attila, Casiornis, Rhytipterna* y *Laniocera* parecen estar mas relacionados con las Tyrannidae, especialmente con *Myiarchus,* que con las coloridas cotingas, entre las cuales están usualmente incluídos. Se diferencian de éstas por poseer músculos oblicuos y cartílagos internos. Los picos gruesos (*Pachyramphus* y *Platypsaris*) también parecen pertenecer a las Tyrannidae.
3) Entre las Tyrannidae (atrapamoscas tiranas), la siringe se caracteriza por la presencia de músculos intrínsecos oblicuos y cartílagos internos. Hay varios grupos estructurales, variando en homogeneidad. En general estos grupos respaldan la clasificación de Hellmayr (1927).
   a) *Sayornis* se acerca más a *Empidonax* y *Nuttallornis* que al grupo *Fluvicola.*
   b) *Myiozetetes, Sirystes* y *Legatus* parecen estar mal colocados en su posición actual, en medio de una serie linear que incluye *Muscivora, Tyrannus, Empidonomus, Myiodynastes, Megarhynchus, Pitangus* y *Tolmarchus.*
   c) La subfamilia Platyrinchinae, caracterizada por picos anchos y aplastados, parece ser una agrupación artificial, considerando las amplias diferencias de estructura en la siringe de los tres géneros (entre cinque) estudiados.
   d) Los géneros *Terenotriccus, Pyrrhomyias, Myiobius* y *Onychorhynchus,* junto con el saltarín *Piprites,* forman un grupo caracterizado por la ausencia de músculos intrínsecos y (en la mayoría) por asimetría de la siringe.
4) El picoagudo (*Oxyruncus*) posee músculos oblicuos intrínsecos y cartílagos internos característicos de los Tyrannidae, pero los detalles de la siringe no son de mucha ayuda para determinar los nexos más cercanos que tiene el picoagudo dentro del grupo de las atrapamoscas tiranas.
5) Tres familias pequeñas del Antiguo Mundo, las Pittidae, las Philepittidae y las Acanthisittidae, son corrientemente colocadas en el suborden Tyranni a base unicamente de la estructura de la siringe, pero no muestran ninguna relación obvia con ninguna de las familias del Nuevo Mundo. La siringe de las Philepittidae es notablemente parecida a la de los picoanchos *Psarisomus* y *Serilophus,* con los cuales *Philepitta* comparte ciertas características del esternón y del pterylosis. Es muy posible que las Philepittidae estén relativamente más cerca de las Eurylaimidae que de los Tyranni o los Furnarii.

6) Los pájaros-rastrojeros (Atrichornithidae) son más parecidos a los pájaros cola de lira (Menuridae) en la estructura de la siringe de lo que antes se creía. Ambos tienen tres pares de músculos intrínsecos, colocados de una manera muy parecida a la de los pájaros canoros (Passeres).
7) El suborden Passeres ha sido estudiado extensamente. Es mucho menos variable en la estructura de la siringe que los Tyranni o los Furnarii. La siringe es compleja pero uniforme en todo el suborden, sugiriendo que el grupo pueda ser estrechamente monofilético. La ausencia del pessulus en las alondras (Alaudidae) no debe considerarse como carácter primitivo, puesto que su falta es muy probablemente una condición secundaria. El pessulus está presente en casi todos los suboscines y también en los órdenes no-paserinos Piciformes y Coraciiformes; muy probablemente estaba presente en la forma ancestral de los Passeres.

РЕЗЮМЕ

РЕЗЮМЕ

Нижняя гортань (сринкс) уже свыше столетия считается важным органом при установлении подразделений птичьего отряда Passeriformes (воробьиных); она сейчас изучена у 983 экземпляров, представляющих собой 65 семейств из тех 67, которые признаны большинством современных авторитетов. Особое значение придавалось подотряду Tyranni и, главным образом, семейству Tyrannidae (тираннов).

Три общие морфологические категории, установленные Мюллером в 1847 г., являются основанием для главных подразделений, которыми пользуются теперь. Из трёх разрядов Мюллера, два представляют, повидимому, обоснованные таксономические разряды: "Tracheophonae" (современное надсемейство Furnarioidae) и "Polymyodae" (подотряд Passeres или певчих воробьиных, называемый часто певчими птицами). Третий разряд Мюллера "Picarii" содержит как простые, так и сравнительно сложные виды нижних гортаней птиц. Таксономические решения, основанные на свойствах нижней гортани простого вида (у которой отсутствуют внутренние мышцы и хрящевые утончения) следует делать осторожно, так как простой тип нижней гортани представляет, повидимому, наследственную "дятло-воробьиную" нижнюю гортань. Некоторые результаты данного исследования наводят на мысль о внесении изменений в современную классификацию Passeriformes.

1) Совокупность птиц муравьеловок и печников, которая в настоящее время рассматривается, чаще всего, как надсемейство (Furnarioidea) в подотряде Tyranni следует возвысить в ранг подотряда (Furnarii). Эта группа отличается крайней специализацией голосового аппарата, что отделяет её от других воробьиных. Кроме того отсутствуют какие бы то ни было структурные особенности, которые связывали бы эту группу, в частности, с другими воробьиными.
   a) Furnariidae (печники) состоят в ближайшем родстве с Dendrocolaptidae (древолазы Южной Америки), но могут быть отделены от них ввиду отсутствия (за исключением у Geositta) спинных и брюшных "рогов" на Processi vocales. Formicariidae (муравьеловки) делятся на две группы строения, что обусловлено несколькими особенностями нижней гортани, которые подкреплены внешними деталями. Эти группы можно назвать: "типичными муравьеловками" (Thamnophilus и др.) и "наземными муравьеловками" (Grallaria, Conopophaga и др.).

2) Cotingidae (котинги), согласно классификации существующей в настоящее время, охватывают несколько типов нижних гортаней.
   a) Attila, Casiornis, Rhytipterna и Laniocera состоят, вероятно, в более близком родстве с Tyrannidae и в особенности с Myiarchus, чем с более красочными котингами, к которым их обыкновенно относят, но от которых они отличаются тем, что имеют наклонные внутренние мышцы, а также и внутренние хрящи.
   b) Бекарды (Pachyrampus и Platypsaris) тоже относятся, повидимому, к Tyrannidae.

3) У Tyrannidae (тиранков) нижняя гортань характеризуется наличием наклонных внутренних мышц и внутренних хрящей. Существует несколько структурных групп, степень однородности которых не одинакова. Вообще же эти группы подтверждают классификацию Hellmayr (1927).
   a) Sayornis находятся, вероятно, в более близком родстве с Empidonax и Nuttallornis, чем с группой Fluvicola.
   b) Myiozetetes, Sirystes и Legatus, очевидно, не следует помещать в середине линейной серии, включающей Muscivora, Tyrannus, Empidonomus, Myiodynastes, Megarhynchus, Pitangus и Tolmarchus.
   c) Подсемейство Platyrinchinae, которое характеризуется широкими и плоскими клювами, кажется искусственный конгломератон, если принять во внимание значительные различия в устройстве нижней гортани и трёх видов (из пяти), которые были изучены.
   d) Виды Terenotriccus, Pyrrnomyias, Myiobius и Onychorhynchus, наряду с манакинами Piprites, образуют группу, которая отличается отсутствием внутренних мышц и (у большинства) асимметрией нижней гортани.

4) Остроклюв (Oxyruncus) имеет и наклонные внутренние мышцы, и внутренние хрящи, характерные для Tyrannidae, однако, детали нижней гортани мало помогают диявняскение толо, с какой группой тираннов остроклюв состоит в ближайшем родстве.

5) Три небольших семейства Старого Света, Pittidae, Philepittidae и Acanthisittidae, относимые в настоящее время к подотряду Tyranni, всецело на основании строения их нижних гортаней, не имеют явной связи с каким бы то ни было семейством Нового Света. Нижняя гортань Philepittidae замечательно похожа на нижнюю гортань ширококлювов Psarisomus и Serilophus, с которыми у Philepitta имеется ряд общих черт в устройстве грудины и птерилия. Вполне возможно, что Philepittidae находятся в более близком родстве с Eurylaimidae, чем с Tyranni или с Furnarii.
6) Строение нижней гортани у атрихий (Atrichornithidae) и у лировостов (Menuridae) более однородно, чем предполагалось раньше. У обеих гортаней три пары внутренних мышц, расположенных по типу, который напоминает во многих отношениях устройство нижней гортани у певчих птиц (Passeres).
7) Подотряд Passeres подробно изучен. Различия в устройстве нижней гортани у этих птиц гораздо менее значительны, чем у Tyranni или у Furnarii. Нижняя гортань сложная, но однородная у всего подотряда, что указывает на строгую монофилию группы. Отсутствие у жаворонков (Alaudidae) поперечной болтоподобной кости или хряща при разветлении трахеи на бронхи (pessulus — болт) не следует считать признаком примитивности, так как почти наверняка отсутствие её явствовать вторичный признанный. Болтоподобное устройство существует у большинства представителей подотряда певчих птиц, а также и у неворобьиных отрядов Piciformes и Coraciiformes, по всей вероятности, оно имелось и у предков Passeres.

HISTORY OF SYRINGEAL MORPHOLOGY

The syrinx was first described by Herissant (1753) who recognized it as the source of voice in the domestic duck. Vicq D'Azyr (1779) described the passerine syrinx for the first time and believed that the syrinx of songbirds represented the simplest form. Cuvier (1802) examined the syrinx of the European Starling (*Sturnus vulgaris*), concluding that its morphology was far more complex than suggested by Vicq D'Azyr. Savart (1826) described the syrinx of songbirds in more detail, naming the muscles on the basis of their action. He noted a membrane extending anteriorly from the pessulus and called it the "*Membrana semilunaris.*" Yarrel (1833) examined the syrinx of the Raven (*Corvus corax*) but added little to previous descriptions.

Nitzsch (1829) described the syringes of many European passerines and non-passerines. He was the first to apply syringeal morphology to the classification of birds. In this he was not very successful, but he did show that the "singing birds" have a strongly muscled syrinx.

The earliest descriptions of the syrinx in New World passerines, including many of the Tyranni, were those of MacGillivray (1838). He described the vocal organs of *Tyrannus, Myiarchus, Contopus,* and *Empidonax* and noted that the pessulus is lacking "in *Tyrannus* as in all the New World Muscicapidae." He also described the syringeal structure in thirty-nine genera of oscines, belonging to many families. MacGillivray's examination was frequently of a superficial nature, as indicated by his belief that the principal differences in syringeal structure were in the degree of development. Blyth (1838) examined the vocal organ in a few cotingas, manakins, and tyrant flycatchers and concluded, after a rather superficial examination, that it was as complex as that of European passerines.

Eyton (1841-1844) produced the first description of the "tracheal" syrinx in *Upucerthia, Furnarius, Cinclodes,* and *Synallaxis.* In other papers he described the Lyrebird *Menura* (1841) and *Gymnorhina* (1842). Like many of his predecessors, Eyton apparently suffered from inadequate magnifying equipment, for in *Menura* he overlooked a pair of muscles later described by Garrod (1876). Eyton was primarily interested in the Mm. sternotracheales and in a great number of cases he "described" the syrinx entirely in terms of these muscles.

Müller (1847, 1878) examined the syringes of more genera of birds than anyone before him. He separated the "American Muscicapidae" (Tyrannidae) from the Old World (true) Muscicapidae on the basis of the degree of development of their syringeal muscles. He was the first to provide a systematic arrangement of the Passeriformes based on syringeal morphology, and to relate the form of the syrinx to other anatomical characters, particularly the scutellation of the tarsus. Müller's work has been the foundation for all subsequent classifications in which the syrinx has been used as a taxonomic character.

Herre (1859) and Owen (1866) described the syringeal structure of many European passerines, but added little new information. Owen's nomenclature for the oscine syringeal muscles has been used by most subsequent writers in English.

Garrod (1876, 1877a) described the syrinx of many non-oscine genera, including *Menura, Atrichornis, Pitta,* and several other Tyrannoidea. He coined the terms "mesomyodian" and "acromyodian," referring to the position of the insertion of the intrinsic muscles. Forbes, a pupil of Garrod, described the syrinx in the broadbills *Eurylaimus* and *Cymbirhynchus* (1880a), in *Acanthisitta* and *Xenicus* (1882), in *Conopophaga* (1881), and in *Philepitta* (1880b). The study of *Acanthisitta* was repeated by Pycraft (1905a).

Wunderlich (1886) described the syrinx in a large number of European birds, including a few passerines. His most significant contribution was in the embryology of the syrinx, which he studied in the domestic duck and in the House Sparrow (*Passer domesticus*). Furbringer (1888) summarized the work of previous authors and coined the word "diacromyodian" for the condition in which the muscles insert at both ends of a single element.

Gadow and Selenka (1893) collated the findings of previous authors and provided an original description of the syrinx in the European Crow (*Corvus corone*). Because their description and nomenclature were to be so extensively used by later investigators, it is particularly unfortunate that their illustrations of *Corvus* contain four errors in labeling muscles.

Haecker (1900) was primarily interested in the means and function of sound production. With histological sections he demonstrated differences in muscles and in cartilages between sexes and age groups in several species of European passerines.

Setterwall (1901) studied the syringeal structure of a large number of Palearctic songbirds. He concerned himself with some of the less studied aspects of the syrinx, such as individual variation. He looked carefully at the interior of the syrinx and was particularly interested in the small cartilaginous elements. Setterwall's theories on the function of the syrinx were to have considerable effect on the studies of Rüppell (1933) and Greenewalt (1968).

By the turn of the century it was a common practice to include a description of the syrinx in the systematic morphology of a species. More often than not, such inclusions were exeremely brief, such as Pycraft's (1905b) mention that the syrinx of the Wren Thrush (*Zeledonia*) is "typically oscine." It was the beginning of an era in which many passerines were to be classified largely on the basis of syringeal structure. Bates (1914) used the morphology of the syrinx of *Smithornis stongei* to remove that genus from the oscine family Muscicapidae and ten years later Lowe (1924) compared the syrinx of *S. rufolateralis* with that of *Eurylaimus*, in placing *Smithornis* in the Eurylaimidae. The rare Grauer's Broadbill (*Pseudocalyptomena*) was placed by Lowe (1931) in the Eurylaimidae on the basis of the syrinx and some other characters.

Köditz (1925) studied the syringeal morphology in a number of species of the families Pycnonotidae, Meliphagidae, Nectariniidae, Irenidae, Zosteropidae, Pittidae, and Eurylaimidae. He pointed out that apparent variations in the number of oscine syringeal muscles are more often due to differences in nomenclatorial concepts than to actual differences in syringeal structure.

Maynard (1928) studied the syrinx in a number of passerines and non-passerines, taking careful measurements of many parts of the respiratory system. Unfortunately, his book is illustrated with woodcuts which give only a vague impression of syringeal structure. His apparent lack of good magnifying equipment is indicated by the many inaccuracies in the descriptions.

The twentieth century has seen a number of passerine genera moved from one suborder to another, partly or wholly on the basis of syringeal morphology. *Melampitta* (Mayr, 1931), *Lawrencia* (Wetmore and Swales, 1931), and *Ramphocaenus* (Wetmore, 1943) were shown to be oscines. *Psilorhamphus*, thought to be a close relative of *Ramphocaenus*, was proven by Plótnick (1958) to belong in the furnarioid family Rhinocryptidae. Amadon (1951) showed through syringeal morphology that the Madagascar genus *Neodrepanis* is not oscine, but closely related to the peculiar Asities (Philepittidae).

The systematic positions of some passerines have been confirmed by syringeal morphology. The syrinx of the extinct Mascarene starling *Fregilupus* was described by Miller (1941) and in more detail by Berger (1957) who compared it with that of the Vanga Shrike *Artamella* and with the European Starling *Sturnus*. After comparing the syrinx of *Gymnorhina* with that of *Corvus*, Mayr (1931) affirmed that the Cracticidae are more closely related to the Corvidae than to the Laniidae. Mayr and Amadon (1951) examined the syrinx of the African River Martin *Pseudochelidon* and concluded that it merited subfamily separation from the other swallows.

In a lengthy paper devoted largely to the mechanics of sound production in non-passerines, Rüppell (1933) described the syrinx of the woodhewer *Lepidocolaptes*, naming the intrinsic muscles for the first time. Clark (1913) compared the syrinx of the Sharpbill *Oxyruncus* with that of the tyrannid *Sayornis*, concluding that the Sharpbill is a modified tyrannid. Kuchler (1936) used the morphology of the syrinx in the Plantcutter *Phytotoma* to relate that genus to the Cotingidae. Lowe (1942) used syringeal morphology to indicate evolutionary trends in some Pipridae.

One of the most significant studies of the passerine syrinx in recent years is that of Miskimen (1951), in which the vocal organs of twenty-nine oscine species and two tyrannids were described. Her statements on the range of variation in number of syringeal muscles among North American songbirds differed greatly from the accounts of Wunderlich, Haecker, Setterwall, and Köditz, all of whom studied Old World species. Miskimen's findings indicated that the total number of muscles varies from four to seven pairs and these figures have been linked to Setterwall's upper limit of nine pairs to suggest greater variability than was previously believed present. Miskimen performed *in vitro* experiments on the syrinx, repeating some of Rüppell's (1933) experiments. She was able to confirm that sound is produced on the expirant cycle of respiration and to show that the *membrana semilunaris* plays only a minor role in sound production.

In a more recent paper (1963) Miskimen described the syrinx in six genera of the Tyrannidae. She provided the most thorough description of the tyrannid syrinx to date and was the first to show clearly the oblique character of the ventral intrinsic muscles.

Greenewalt (1968) analysed the vocalizations of a wide spectrum of non-passerine and passerine birds. In addition to a detailed discussion of the acoustics of bird song,

he set forth an hypothesis for the mechanism of sound production and modulation. Stein (1968) also analysed a number of bird vocalizations and proposed a theory of the operation of the syrinx, differing from that of Greenewalt on several points.

Chamberlain et al. (1968) studied the syrinx of the North American Crow (*Corvus brachyrhynchos*), with particular regard to the action of various muscles and their possible effect on the syringeal membranes.

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METHODS AND MATERIALS

METHODS OF DISSECTION AND PREPARATION.

The syrinx in passerine birds lies immediately anterior to the heart, surrounded by the interclavicular air sac. Descending the right side of the neck, the trachea enters the air sac at the base of the neck and shortly divides into the bronchi. The esophagus, which lies dorsal to the trachea for most of its length, passes between the bronchi near the tracheobronchial bifurcation. A small fibrous sheet, the bronchidesmus, joins the inner walls of the bronchi to the ventral surface of the esophagus. A tough silvery sheet, which Setterwall (1901) called the "syringeal aponeurosis," forms the anterior and dorsal walls of the air sac and is firmly attached to the trachea where the latter penetrates the air sac. The syrinx, located at the tracheobronchial junction, is too deep in the body cavity for study *in situ*. The use of formalin-preserved specimens facilitates the study of the minute syringeal muscles, which become firmer and easier to work with. Moreover, the majority of passerine birds are available only in anatomical "spirit" collections.

Many anatomists have found it convenient to remove the entire trachea, as well as the larynx and the tongue, for the study of the syrinx alone. In doing so they destroy most of the hyoid apparatus, which is itself of anatomical interest. I prefer a system of dissection that insures that the syrinx will be removed undamaged, while minimizing the damage to neighboring systems. Only the lower trachea, syrinx, bronchi, and a small section of esophagus are removed.

Once the interclavicular air sac has been opened and a visual inspection made to determine that the syrinx has not been destroyed by shot, which it occasionally is, a sagittal cut is made in the sternum and pectoral muscles a few millimeters to the right of the keel. In large birds (over 150 gm.) the sternal cut is omitted, unless the specimen is easily replaced. Next the trachea and esophagus are severed at the middle of the neck. A small scissors is used to cut the Mm. sternotracheales midway between origin and insertion. Failure to perform this cut usually results in the muscles being torn from the syrinx, where the attachment is often weak. The major blood vessels are now cut where they lie ventral to the bronchi (in large birds this cut can sometimes be omitted). A careful transverse cut across the posterior ends of the bronchi and esophagus frees the section of the respiratory and digestive tracts to be removed. With thin blunt forceps one can now lift the esophagus from the tissues dorsal to it and draw it anteriad, cutting the restraining connective tissue with a scalpel or fine scissors. By pulling only on the esophagus one draws the syrinx with it, minimizing the likelihood of damage to the syrinx.

In many large birds the size of the interclavicular air sac is sufficient to permit the removal of the syrinx with dental instruments, without cutting the sternum. Particularly necessary in this type of removal is a small scalpel, the blade of which lies in a plane at right angles to the handle. Considerably more time and care is needed, but

the only significant damage to other organ systems is to the arteries of the region surrounding the syrinx.

After removal from the bird the syrinx is placed in a small dissecting dish for examination under binocular magnification of 20-60 ×. Usually some "clean-up" is necessary, removing preserved blood and body fluids, and peeling off the fine membranes which cover and obscure the muscles and cartilages. For gentle removal of unwanted surface material a fine artist's brush (00000 or smaller) is useful, aided by a jeweler's forceps. For further dissection I employ a variety of small scalpels and probes, ground from dental instruments.

For long-term storage, syringeal specimens are kept in an aqueous solution of 65 per cent ethanol and 10 per cent glycerine.

NOMENCLATURE.

Cartilaginous Elements.

In all passerines the middle of the trachea lies on the right side of the neck, twisted and laterally displaced relative to its ends. The dorsoventral orientation of the ends of the trachea corresponds to that of the bird, but in the middle section the "dorsal" side (determined by the position of the lateral muscles and nerves) lies against the side of the neck. The terms "ventral," "dorsal," "medial," and "lateral" are used here with respect to an idealized straight trachea, ignoring torsion and bending.

Previous authors, from Müller to Miskimen, have numbered the cartilaginous elements in two series, "tracheal" and "bronchial," numbering away from the point where the series meet. This point is the theoretical "tracheo-bronchial" junction. Traditionally those elements which are full circles are "tracheal rings"; those composed of paired semicircles or of two separate coplanar circles are "bronchial" semirings or rings. On this basis two individuals of the same species may appear to differ widely merely because fusion of elements has produced different starting points for the series. In the examination of the syringes of 784 species of 531 genera, I have found it impossible to name the supporting elements in the historical tracheal-bronchial sense. The elements do fall into two series, which I designate "A" and "B", based on the following criteria (see Pl. 1, fig. 2):

1) Cross section.
   Type A: flat and ribbon-like
   Type B: round or D-shaped
2) Consistency.
   Type A: transparent and stiff, often brittle
   Type B: whitish and opaque; spongy and flexible
3) Direction of concavity, other than toward axis of tube.
   Type A: directed posteriad
   Type B: directed anteriad

The A-series is always the more anterior of the two and, with no known exceptions, each series is continuous. Each series is numbered away from the point where the series meet.

The borderline between cartilage and bone in the passerine syrinx is not a sharp one. Very little true histological work was done in this study and the degree of ossification has not been quantitatively determined. Miskimen (1963) stated that, unlike the bony tracheal elements of the oscines, those of the Tyrannidae are cartilage. Some of the syringes of cotingas received from William Beebe, however, had been previously stained with alizarin using the method of Hollister (1934), which indicated the presence of calcium. The application of Von Kossa's Stain to sections of an adult phoebe syrinx (*Sayornis*) also indicated calcification of the tracheal elements, although less than in the Beebe specimens. Because the amount of calcification is much less than in the axial skeleton and because further histological work is needed to clarify the question, I will refer to all of the supporting elements of the syrinx as "cartilaginous."

The terms "ring" and "semiring," used by most authors to describe, respectively, the closed circular and the open semicircular elements, are inadequate to describe the variety of supporting cartilages in the passerine syrinx. The following adjectives are defined in the context of this paper (Pl. 1, fig. 1.):

1) Complete. The element forms a closed circle or ellipse.
2) Incomplete dorsally (or ventrally). The element forms a complete circle or ellipse except for a single opening near the dorsal (or ventral) midline.
3) Divided. The element consists of two halves, separated by openings near the dorsal and ventral midlines. The halves are mirror images, lie at approximately corresponding points relative to the tracheal axis, and are arcs of circles.
4) Double. The element consists of paired components, each of which is a closed loop. The loop need not be circular; the commonest type is D-shaped with the flat side directed medially. The halves may be 1) connected, i.e. fused more or less firmly in the region of contact, or 2) discrete, i.e. if in contact, able to move freely relative to each other.

When reference is made to one half of a divided or a double element the smaller part is termed a component, the word "element" being reserved for the entire structure. Reference to the right or left half of an element is indicated by an appropriate "R" or "L" added to the number of the element, viz: A-2R.

Unpaired components do occur, appearing as extra halves added to an otherwise symmetrical system. Such components are numbered with an "a" added to the number of the next lower element, and R or L to indicate the side. A-4aL is an unpaired component lying between A-4 and A-5 on the left side.

The pessulus is a bony or cartilaginous rod or narrow plate lying in the midsagittal plane of the trachea at the junction of the internal tympaniform membranes. Usually it is fused to other elements at its dorsal or ventral end, frequently at both. It may bear a small midsagittal membrane directed anteriorly, the *Membrana semilunaris.*

The drum is a cylinder composed of two or more complete A-elements fused along their entire lengths. Frequently the fusion is so complete that no seams remain to indicate how many elements comprise the drum. Miskimen (1963) used this term to designate the most posterior complete element or group of elements, in case of fusion. Functionally, a drum of fused elements provides a rigid support against compression of the trachea by muscles, so the term is inappropriate for a single unmodified element.

A *labium* is a cartilaginous pad or bar projecting into the lumen of the bronchus from the lateral ("*externum*") or medial ("*internum*") side. The *labia externa* are attached to the inner side of an A- or B-element; the *labia interna* are attached to the

pessulus or are histologically continuous with it. Since my study did not usually involve opening the trachea or bronchi, the characteristics of the labia were seldom noted. What I have called the "cartilaginous plug" in the tyrannid syrinx may, in fact, be the result of extension and coalescence of the internal labia.

Membranes.

Although the entire inner surface of the respiratory tract is a continuous epithelium, and another membranous sheet covers muscles and cartilaginous elements, in discussions of gross morphology the word "membrane" has traditionally been applied to a region between cartilaginous elements. In this sense, rather than a strictly histological one, the word is used here. Syringeal membranes vary in thickness and flexibility, sometimes blending imperceptibly into sheets of cartilage. Each discrete area of membrane is labeled by the elements surrounding it, the membrane between A-1 and B-1 being the "A-1/B-1 membrane."

Internal tympaniform membranes. This pair of membranes comprises most of the internal surface of the bronchi. They are supported at their edges by the ends of the divided A and B elements.

External tympaniform membranes. This name has usually been applied to the largest of the membranous areas on the lateral sides of the syrinx. The word "tympaniform" is inappropriate in most cases and the size of the membranes in preserved specimens is greatly influenced by the position of the syrinx in fixing. The term is not used in this paper.

Muscles.

The following muscles are extrinsic; they originate away from the syrinx and insert on it. Both are paired muscles. The terms "extrinsic" and "intrinsic" are used here with reference to the syrinx, not to the entire trachea, as is sometimes the case. An intrinsic tracheal muscle is an extrinsic syringeal one if it originates on a non-syringeal part of the trachea.

M. tracheolateralis. This thin, usually narrow muscle originates on the lateral surface of the cricoid cartilage of the larynx. It extends down the lateral surface of the trachea to insert on the ventral and/or lateral surfaces of one or more elements in the syringeal region.

M. sternotrachealis. This muscle originates on the internal surface of the coracoid or the costal process of the sternum, or on the internal surface of one or more ribs. Rarely, it originates on the inner surface of the intercostal muscles. It inserts on the lateral and/or ventral surface of the trachea, or on the tissues surrounding the trachea. Sometimes M. sternotrachealis is wholly or partly continuous with some of the fibers of M. tracheolateralis. Plótnick (1958) renamed this muscle M. costotrachealis in certain of the Furnarioidea, on the basis of its costal origin. While the new name is accurately descriptive, the basic position of the muscle is the same in the Furnarioidea as in virtually all other birds and the addition of the new name serves no useful purpose.

SOURCE OF SPECIMENS.

Most of the 983 specimens dissected in the course of this study were obtained from the alcohol collections of the Peabody Museum of Natural History (YPM), the United States National Museum (USNM), and the American Museum of Natural History (AMNH). The source of each specimen in the suborders Eurylaimi, Tyranni, and Menurae is given with the data in Appendix A. The details of the syringeal morphology of most of the oscines will be discussed in a series of future papers; only the names of the oscine species are given in Appendix B.

SYSTEMATICS USED IN THE MORPHOLOGICAL SECTION.

In the morphological sections that follow, the specimens are presented in taxonomic order, based on the prevailing classification of the present time. The arrangement of suborders, superfamilies, and families is that of Wetmore (1960). Below the family level there is no taxonomic revision covering the whole order Passeriformes. The most recent classification of the Eurylaimi, and the one followed here, is that of Peters (1951). For the New World Tyranni I have followed Hellmayr (1925-1929), except for the few cases in which a genus or species has been shown to have been placed by Hellmayr in the wrong superfamily or family. I have departed from Hellmayr's classification in including *Rupicola* in the Cotingidae. The nomenclature for the two species of the Menurae treated was drawn from Cayley (1931). For the Passeres I have employed the classification in available volumes of the *Checklist of Birds of the World* (Mayr and Greenway, 1960, 1962; Mayr and Paynter, 1964) and have filled the gaps from recent family revisions and regional works. (See references cited in the appropriate sections of Appendix B.)

The reader will find several instances in which generic names or allocations of species to genera and families are not what he would consider "prevailing classification." Such instances are frequent in Hellmayr's treatment of the Tyranni, which was followed closely on the grounds that the reader may always return to Hellmayr's work to clarify individual problems. In citing anatomical studies by previous authors, principally those of Müller (1847, 1878) and Garrod (1876, 1877a, b) I have employed the modern generic and specific names.

SYRINGEAL MORPHOLOGY

SUBORDER EURYLAIMI.

FAMILY EURYLAIMIDAE. BROADBILLS.

Specimens Examined.

Of the 14 species in eight genera, I have examined the following seven species in six genera:

Smithornis capensis (A. Smith)
Smithornis rufolateralis G. R. Gray
Cymbirhynchus macrorhynchus (Gmelin)
Eurylaimus javanicus Horsfield
Serilophus lunatus (Gould)
Psarisomus dalhousei (Jameson)
Calyptomena whiteheadi Sharpe

I know of only the following descriptions by previous authors:

Cymbirhynchus macrorhynchus (Gmelin) — Forbes (1880a)
Eurylaimus ochromalus Raffles — Forbes (1880a)
Pseudocalyptomena graueri Rothschild — Lowe (1931)
Smithornis sharpei Boyd Alexander — Bates (1914)
Smithornis sharpei Boyd Alexander — Lowe (1924)
Smithornis capensis (A. Smith) — Verheyen (1953, p. 184)
Smithornis rufolateralis G.R. Gray — Lowe (1924)
Corydon sumatranus (Raffles) — Müller (1847, p. 32; 1878, p. 27)

Müller's "description" of the syrinx of *Corydon* is merely a note on the lack of musculature.

Cartilaginous Elements.

In all species of *Smithornis* the cartilages are closely similar. A-1 and A-2 are divided, A-2 being oriented at an angle of about 45° to the sagittal plane of the trachea. A-3 and other A-elements are complete and all the B-elements are divided. There is no pessulus. My specimens agree closely with those of Lowe and, except for one detail, those of Verheyen. The latter was the only author to describe a drum in a broadbill. He does not state which elements are involved, but from his illustration and his statement that the drum has strengthening rings of "bronchial origin," it appears that the drum occupies the region of A-1 through A-3. In my specimens the A-1/A-2 and A-2/A-3 membranes are thick and leathery, but quite flexible. Verheyen's statement that the drum is continuous dorsally with the "bronchio-pulmonary" membranes leads me to believe that the "drum" was an artifact of preparation.

Eurylaimus and *Cymbirhynchus* are like *Smithornis,* with the following differences. A-1, described by Forbes as a "false ring," is shorter than B-1 and A-2 and floats in the membrane bounded by them. B-1 and A-2 are held together at their dorsal and ventral ends by fibrous connective tissue. The ventral half of A-1 is very narrow, about one quarter the width of the dorsal end, where it is as wide as the other A-elements. The pessulus is fused to A-3 at its dorsal and ventral ends. In the specimen of *Cymbirhynchus* illustrated by Forbes (1880a), A-3 seems to be incomplete dorsally and the pessulus is continuous with the dorsal end of A-3L. In other respects Forbes' specimen is similar to mine. In both specimens A-1 through A-6 are fused midventrally.

Psarisomus (Pl. 2) and *Serilophus* are like *Smithornis,* with the following differences. A-1 is divided and closely fitted to A-2, which is complete. At its dorsal end A-1 is broadly spatulate and is twisted so that its internal (concave) surface is directed posteriad. The whole arc of A-1 is at an angle of about 30° with the sagittal plane. A-2 is very narrow laterally but has large, triangular dorsal and ventral surfaces, filling the area between A-1 and the unmodified A-3. At its posterior ends A-2 is continuous with the narrow pessulus.

Lowe's description of *Pseudocalyptomena* suggests a strong similarity to *Psarisomus.* He found some fusion of "the last two or three tracheal rings," probably A-2 through A-4. The pessulus was fused to A-2.

Calyptomena (Pl. 2) is different from the other broadbills. A-1 through A-3 are divided and A-4 is incomplete ventrally. The four elements are fused dorsally to a broad plate extending ventrally into the interbronchial region as a wide pessulus. The posterior borders of this plate are soft white cartilage and blend gradually into the internal tympaniform membranes.

Musculature.

My two specimens of *Smithornis* differ only slightly in their musculature. M. tracheolateralis inserts on the lateral surface of A-5 in *S. capensis,* and on the ventrilateral surface of A-4 in *S. rufolateralis.* In *S. sharpei* Bates (1914, p. 496) noted that the muscle "goes as far as the bronchus," presumably meaning A-2, the most anterior divided element. Lowe (1924, p. 280) stated that "no muscles could be made out attached to the lower end of the trachea or the bronchi" and Verheyen agreed with him.

M. sternotrachealis was hardly mentioned by the above authors. In *S. capensis* it extends through the center of M. tracheolateralis and is continuous with the deep fibers of the latter. In *S. rufolateralis* it is the superficial fibers of the dorsal half of M. tracheolateralis with which M. sternotrachealis is continuous.

In *Eurylaimus* the insertion of M. tracheolateralis is on the center of A-2. In *Psarisomus, Serilophus* and *Calyptomena* it inserts midlaterally on A-1. In *Cymbirhynchus* the insertion is by a broad tendon to the center of B-1. The fibers of the muscle end at A-2, but when the muscle is lifted the tendon becomes evident. Forbes' description and illustration of this muscle inserting on A-2 are probably in error. Of *Corydon sumatranus,* Müller stated only that muscles are lacking on the lower trachea, implying a condition like that of *Smithornis.* In *Pseudocalyptomena* Lowe described a pair of "intrinsic muscles," apparently inserting on A-1. It is evident from the description and the accompanying illustration that this pair are the Mm. tracheolaterales, and that there are no intrinsic muscles in the usual sense.

M. sternotrachealis is more variable in its form of insertion. In *Eurylaimus* it is wholly continuous with M. tracheolateralis, which it meets at A-8. In *Serilophus* the anterior fibers of M. sternotrachealis are continuous with the superficial ones of M. tracheolateralis and the posterior fibers insert directly on A-11 and A-12. In *Psarisomus*, M. sternotrachealis divides into two fasciculi, which insert directly on A-10 and A-11 at the ventral and dorsal edges of M. tracheolateralis, respectively. In *Calyptomena* the right muscle is similar to that of *Psarisomus*, inserting on A-9 and A-10; the left extends intact through a split in M. tracheolateralis to insert directly on the same elements. In *Cymbirhynchus* the insertion of M. sternotrachealis covers a circular area on A-8 and A-9, adjacent to the dorsal edge of M. tracheolateralis.

Suborder Tyranni.

Superfamily Furnarioidea.

NOMENCLATURE.

The nomenclature listed on p. 14 applies here, with the following additions:

1) Cartilaginous elements.

Processus vocalis. A cartilaginous or partly ossified plate covering part of the lateral surface of the posterior trachea, anchored by fusion or by fibrous connective tissue to the lower A-elements. It frequently has projecting "horns" (the *processi musculares* of Müller, 1847) to which muscles are attached.

2) Membranes.

Membrana trachealis. This is a membranous window on the ventral and/or dorsal surface of the trachea. It is differentiated from the other membranes of the trachea by the fact that it spans the positions of several elements. The Membrana trachealis may be crossed by narrow sections of several A-elements. In such cases the Membrana trachealis may be considered to be the sum of the series of smaller membranes.

3) Muscles.

M. vocalis ventralis. This name was applied by Rüppell (1933) to the ventral intrinsic muscle of *Lepidocolaptes fuscus*. It originates on the lateral surface of one or more elements anterior to the Membrana trachealis and inserts on the Processus vocalis or on the elements ventral or lateral to the Membrana trachealis.

M. vocalis dorsalis. Rüppell (1933) applied this name to the muscle which occupies a dorsal position corresponding to that of M. vocalis ventralis. It originates on the lateral surface of one or more elements anterior to the Membrana trachealis and inserts on the Processus vocalis or on the elements dorsal or lateral to the Membrana trachealis.

FAMILY DENDROCOLAPTIDAE. WOODCREEPERS.

Specimens Examined.

Of 50 species in 13 genera, I have examined 14 specimens belonging to the following 12 species in nine genera.

Dendrocincla fuliginosa (Vieillot)
Sittasomus griseicapillus (Vieillot)
Glyphorhynchus spirurus (Vieillot), two specimens

Drymornis bridgesii (Eyton)
Xiphocolaptes promeropirhynchus (Lesson)
Xiphocolaptes major (Vieillot)
Dendrocolaptes platyrostris Spix
Xiphorhynchus picus (Gmelin), two specimens
Lepidocolaptes souleyetii (Des Murs)
Lepidocolaptes affinis (Lafresnaye)
Lepidocolaptes albolineatus (Lafresnaye)
Campylorhamphus trochilirostris (Lichtenstein)

I know of only the following descriptions by previous authors:

Dendrocolaptes certhia (Boddaert) — Müller (1847, p. 43; Pl. 6, fig. 12; 1878, p. 35)
Lepidocolaptes fuscus (Vieillot) — Müller (1847, p. 43; 1878, p. 35)
Lepidocolaptes fuscus (Vieillot) — Rüppell (1933, p. 470)

Cartilaginous Elements.

In all the woodcreepers examined the syrinx is dorsoventrally as well as bilaterally symmetrical. In *Dendrocincla* A-1, A-2, and A-3 are divided; A-4, A-5, and A-6 are complete and extremely narrow dorsally and ventrally but of the same width as other elements in the lateral sections. The Membranae tracheales are limited by A-3 and A-7. A-7 and the elements anterior to it are complete and of uniform width. All the B-elements are divided. There are neither a pessulus nor internal cartilages. The Processi vocales are firmly fused to the lateral surfaces of A-1, A-2 and A-3. Well developed horns extend toward the dorsal and ventral midlines in the region of the A-5/A-6 membranes. The most anterior part of the Processus is a round area where M. sternotrachealis inserts, at the level of A-7.

Lepidocolaptes and *Sittasomus* are like *Dendrocincla*, differing as follows. Only A-1 and A-2 are divided; A-3 through A-7 are narrow dorsally and ventrally. The Membranae tracheales extend from A-2 to A-8. A-8 through A-12 are fused into a rigid drum in *Sittasomus* and in *L. souleyetti;* A-8 through A-13 in *L. affinis;* and A-8 through A-14 in *L. albolineatus*. In *L. fuscus* Rüppell reported no fusion and indicated none in his illustration.

Glyphorhynchus is like *Dendrocincla*, differing as follows. A-4 is divided and not narrow. A-5 through A-9 are narrow, the Membranae tracheales extending from A-4 to A-10. In YPM 1802 the drum is formed of A-10 through A-16, but in YPM 1071 it comprises only A-10 through A-13. The horns of the Processus vocalis extend only slightly beyond the main part of the plate.

Xiphocolaptes is like *Dendrocincla,* differing as follows. Only A-1 and A-2 are divided. In *X. major* the Membranae tracheales are like those of *Dendrocincla* but lack the narrow elements extending across them. The drum has the same proportions as that of *Dendrocincla* but fusion is so complete that one cannot count the elements. In *X. promeropirhynchus* the Membranae tracheales extend from A-3 to A-7. The drum consists of A-7, A-8, and A-9.

Campylorhamphus (Pl. 2), *Xiphorhynchus* and *Dendrocolaptes* are like *Xiphocolaptes major*, differing as follows. The drum of *Campylorhamphus* is longer, about nine elements (probably A-10 through A-18) completely fused except for the anterior

two. The Membranae tracheales are proportionately shorter than those of *X. major*. In *Xiphorhynchus* the drum comprises six elements (probably A-10 through A-15) incompletely fused. In *Dendrocolaptes* it appears to be A-9 through A-14.

Drymornis differs from all of the others, principally in the form of the Processi vocales. They are completely fused to A-2 and A-1, both of which are divided. The pair of large components thus formed meets at the dorsal and ventral midlines but articulates freely. The Membranae tracheales are free of cross-elements so that one cannot tell how many elements they span. They are longer and narrower than those of other members of the family. The drum consists of three or four elements, completely fused.

Musculature.

The musculature is the same in all of the woodcreepers examined, with minor variations. M. tracheolateralis extends along the lateral surface of the trachea to insert on the lateral surface of the drum, near its anterior edge. *Dendrocincla* is an exception, there being no drum; the insertion is on A-9. In *Xiphocolaptes promeropirhynchus* the insertion is along a spiral line from A-11 ventrally to A-15 dorsally. In *Glyphorhynchus* the muscle divides into two short fasciculi, which diverge to insert on the ventrilateral and dorsolateral surfaces of the drum.

M. sternotrachealis inserts directly on the anterior quarter of the Processus vocalis in all species.

M. vocalis ventralis and M. vocalis dorsalis show little variation among my specimens. They originate on the lateral surface of the drum, immediately posterior to the insertion of M. tracheolateralis and extend posteroventrally and posterodorsally, respectively, to insert on the ventral and dorsal horns of the Processus vocalis. In my specimen of *Xiphocolaptes promeropirhynchus* a narrow band of the superficial fibers of the right M. vocalis ventralis originates at the dorsal edge of M. tracheolateralis, extends across the latter and across the anterior end of M. vocalis dorsalis to join the rest of M. vocalis ventralis. This is probably an individual variant.

FAMILY FURNARIIDAE. OVENBIRDS.

Specimens Examined.

Of 210 species in 55 genera, I have examined the following 29 individuals in 25 species and 22 genera:

Geositta cunicularia (Vieillot), three specimens
Furnarius leucopus Swainson
Cinclodes patagonicus (Gmelin), two specimens
Cinclodes fuscus (Vieillot)
Upucerthia dumetaria Geoff. Saint Hilaire
Limnornis curvirostris Gould
Aphastrura spinicauda (Gmelin)
Phleocryptes melanops (Vieillot), two specimens
Synallaxis cinerascens Temminck
Certhiaxis cinnamomea (Gmelin)
Asthenes pyrrholeuca (Vieillot)
Phacellodomus rufifrons (Wied)

Phacellodomus striaticollis (Lafr, and D'Orb.)
Anumbius anumbi (Vieillot)
Pseudocolaptes boissoneautii (Lafresnaye)
Pseudoseisura lophotes (Reichenbach)
Pseudoseisura gutteralis (Lafr. and D'Orb.)
Anabazenops fuscus (Vieillot)
Philydor rufus (Vieillot)
Automolus ochrolaemus (Tschudi)
Heliobletus contaminatus Berlepsch
Xenops minutus (Sparrman)
Megaxenops parnaguae Reiser
Pygarrhicus albogularis (King)
Sclerurus guatemalensis (Hartlaub)

I know of only the following descriptions in literature:

Cinclodes nigrofumosus (Cabanis) — Müller (1847, p. 42; Pl. 2, fig. 10; 1878, p. 34)
Furnarius rufus (Gmelin) — Müller (1847, p. 41; Pl. 2, figs. 6, 7; 1878, p. 34)
Furnarius leucopus Swainson — Müller (1847, p. 41; Pl. 2, figs. 8, 9; 1878, p. 34)
Xenoctistes rufosuperciliatus (Lafresnaye) — Müller (1847, p. 42; 1878, p. 34)
Heliobletus contaminatus Berlepsch — Müller (1847, p. 42; 1878, p. 34)
Xenops rutilus Lichtenstein — Müller (1847, p. 43; 1878, p. 35)
Sclerurus fuscus Wied — Müller (1847, p. 42; 1878, p. 35)

Cartilaginous Elements.

The configurations of the cartilages in the Furnariidae examined are summarized in Table 1. Although A-1 and A-2 are uniformly divided, the configurations of other A-elements, of the Membranae tracheales, of the drum, and of the Processi vocales show wide variations. Only the examination of a greater series of individuals and species will permit accurate evaluation of variation. The cartilages of the present 25 species may be summarized as follows:

1) A-1, A-2 and all B-elements are divided.
2) A-3 may be of any configuration except double.
3) A-4 is complete in all except *Synallaxis,* in which it is incomplete dorsally.
4) A-5 and subsequent elements are complete.
5) There are neither a pessulus nor internal cartilages.
6) The Processi vocales are narrow flat bars, usually fused posteriorly to the lateral surfaces of A-1 through A-3. In *Cinclodes* they are fused to A-1 and A-2 only; in *Certhiaxis, Asthenes, Phacellodomus,* and *Automolus* to A-1 through A-4; in *Anumbius* and *Pygarrhicus* to A-2 and A-3 only. In all cases the Processi are connected to the A-elements adjacent to them by elastic connective tissue.
7) Dorsal and ventral horns are present on the Processi vocales only in *Geositta.* No intermediates were found between the prominent horns of *Geositta* and the narrow Processi of the other furnariids.
8) In about half of the species examined the Membranae tracheales are limited posteriorly by A-3, the highest numbered posterior limit being A-6 (*Asthenes*).

The anterior limit varies from A-8 (*Limnornis*) to A-15 (*Automolus*) and does not appear to be correlated with the posterior limit. In other words, the Membranae tracheales consist of from five (*Limnornis* and *Asthenes*) to ten (*Anabazenops* and *Automolus*) smaller membranes. Rarely, the dorsal and ventral Membranae may differ in size (*Aphastrura, Synallaxis, Pygarrhicus*).

9) In the majority of cases all of the elements within the limits of the Membranae tracheales cross the Membranae dorsally and ventrally. Within the Membranae each element is about one-third the width of the unmodified A-elements. In the five cases in which crossbars are lacking (*Cinclodes fuscus, Synallaxis, Certhiaxis, Phacellodomus,* and *Pseudoseisura*) they are absent from the anterior halves of the Membranae only and are widest near the posterior limits.

10) In all but four genera two or more elements immediately anterior to the Membranae tracheales are fused, forming a rigid drum. The number of elements varies from two (*Cinclodes fuscus* and *Megaxenops*) to five (*Limnornis* and *Aphastrura*). Fusion may be complete or partial.

Müller's descriptions agree with the above in all essential points.

Musculature.

In all specimens M. tracheolateralis extends along the lateral surface of the trachea to insert on the anterior edge of the drum or, in the absence of a drum, on the element immediately anterior to the Membranae tracheales. M. sternotrachealis inserts on the anterior end of the Processus vocalis. M. vocalis ventralis originates on the ventrilateral surface of the drum or on the element immediately anterior to the Membranae. It extends ventral to the insertion of M. sternotrachealis and inserts directly on the Processus vocalis. The precise region of insertion is variable. The anterior extreme is in *Sclerurus,* in which it inserts just ventral to the insertion of M. sternotrachealis. The most posterior insertion is in *Furnarius* in which it attaches to the base of the Processus, with a few medial fibers attached to A-2. M. vocalis dorsalis originates on the same element or elements as M. vocalis ventralis, immediately dorsal to the latter, and extends dorsal to the insertion of M. sternotrachealis to attach to the surface of the Processus or, in *Furnarius* only, entirely to A-2. In *Geositta* both of the Mm. vocales insert on the ends of the respective horns of the Processi. In most ovenbirds the dorsal and ventral muscles are of equal length, but in *Heliobletus* M. vocalis ventralis inserts on the Processus at the level of A-5 and M. vocalis dorsalis at the level of A-2.

Müller's descriptions agree closely with the above.

FAMILY FORMICARIIDAE. ANTBIRDS.

Specimens Examined.

Of 234 species in 52 genera (including *Conopophaga* Vieillot[1]), I have examined the following 51 individuals of 33 species in 26 genera:

Cymbilaemus lineatus (Leach), two specimens
Hypoedaleus guttatus (Vieillot)
Taraba major (Vieillot)

[1] *Conopophaga* is included in this family following the conclusions of Ames et al. (1968).

TABLE 1. Configuration of the syringeal cartilages in the Furnariidae.

Genus	A-1	A-2	A-3	A-4	Membranae tracheales ventr.	Membranae tracheales dors.	Crossbars ventr.? dors.?	Drum consists of;	Processi att. to:
Geositta	div.	div.	div.	comp.	A-3 - A-12	same	both	none	A-1 - A-3
Furnarius	div.	div.	i.d.	comp.	A-3 - A-11	same	both	A-11 - A-13	A-1 - A-3
Cinclodes									
patagonicus	div.	div.	div.	comp.	A-3 - A-11	same	both	A-11 - A-13	A-1 - A-2
fuscus	div.	div.	i.v.	comp.	A-3 - A-10	same	neither	A-10 - A-11	A-1 - A-2
Upucerthia	div.	div.	i.v.	comp.	A-3 - A-11	same	both	A-10 - A-12	A-1 - A-3
Limnornis	div.	div.	div.	comp.	A-3 - A-8	same	both	A-8 - A-12	A-1 - A-3
Aphastrura	div.	div.	div.	comp.	A-4 - A-10	A-3 - A-10	both	A-10 - A-14	A-1 - A-3
Phleocryptes	div.	div.	comp.	comp.	A-3 - A-12	same	both	A-12 - A-14	A-1 - A-3
Synallaxis	div.	div.	comp.	i.d.	A-4 - A-11	A-3 - A-11	neither	A-11 - A-12	A-1 - A-3
Certhiaxis	div.	div.	comp.	comp.	A-4 - A-12	same	neither	A-12 - A-15	A-1 - A-4
Asthenes	div.	div.	div.	comp.	A-16 - A-11	same	both	none	A-1 - A-4
Phacellodomus	div.	div.	div.	comp.	A-5 - A-11	same	neither	A-11 - A-12	A-1 - A-4
Anumbius	div.	div.	div.	comp.	A-5 - A-12	same	both	A-12 - A-14	A-2 - A-3
Pseudocolaptes	div.	div.	comp.	comp.	A-3 - A-9	same	both	A-9 - A-12	A-1 - A-3
Pseudoseisura									
lophotes	div.	div.	i.v.	comp.	A-3 - A-11	same	neither	A-11 - A-13	A-1 - A-3
gutteralis	div.	div.	div.	comp.	A-3 - A-11	same	neither	A-11 - A-14	A-1 - A-3
Anabazenops	div.	div.	i.d.	comp.	A-3 - A-13	same	both	A-13 - A-15	A-1 - A-3
Philydor	div.	div.	div.	comp.	A-4 - A-11	same	both	A-11 - A-13	A-1 - A-3
Automolus	div.	div.	i.d.	comp.	A-5 - A-15	same	both	none	A-1 - A-4
Heliobletus	div.	div.	comp.	comp.	A-4 - A-11	same	both	A-11 - A-14	A-1 - A-3
Xenops	div.	div.	div.	comp.	A-3 - A-9	same	both	A-9 - A-12	A-1 - A-3
Megaxenops	div.	div.	i.v.	comp.	A-3 - A-12	same	both	A-12 - A-13	A-1 - A-3
Pygarrhicus	div.	div.	div.	comp.	A-4 - A-10	A-3 - 3-10	both	A-11 - A-13	A-2 - A-3
Sclerurus	div.	div.	comp.	comp.	A-3 - A-11	same	both	none	A-1 - A-3

Sakesphorus canadensis (Linnaeus)
Thamnophilus doliatus (Linnaeus), two specimens
Thamnophilus punctatus (Shaw), three specimens
Thamnophilus caerulescens Vieillot
Pygiptila stellaris (Spix)
Dysithamnus mentalis (Temminck), two specimens
Thamnomanes caesius (Temminck)
Myrmotherula cherriei Berlepsch and Hartert
Myrmotherula axillaris (Vieillot), three specimens
Herpsilochmus pileatus (Lichtenstein)
Microrhopias quixensis (Cornalia)
Neorhopias [= *Formicivora*]*grisea* (Boddaert)
Neorhopias [= *Formicivora*] *rufa* (Wied)
Drymophila squamata (Lichtenstein)
Cercomacra tyrannina (Sclater), two specimens
Pyriglena leucoptera (Vieillot)
Hypocnemis flavescens (Sclater)
Hypocnemoides melanopogon (Sclater)
Myrmeciza exsul Sclater
Myrmoderus squamosus (Pelzeln)
Formicarius analis (Lafr. and D'Orb.), four specimens
Chamaeza brevicauda (Vieillot)
Pithys albifrons (Linnaeus)
Gymnopithys bicolor (Lawrence)
Hylophylax naevioides (Lafresnaye), two specimens
Grallaria varia (Boddaert)
Grallaria perspicillata Lawrence, two specimens
Grallaria ochroleuca (Wied)
Conopophaga lineata (Wied), four specimens
Conopophaga roberti Hellmayr, three specimens

I know of only the following descriptions by previous authors:

Hypoedaleus guttatus (Vieillot)—Müller (1847, p. 39; Pl. 2, figs. 3, 4; 1878, p. 31)
Sakesphorus cristatus (Wied) — Müller (1847, p. 39; Pl. 2, fig. 2; 1878, p. 31)
Thamnophilus doliatus (Linnaeus) — Müller (1847, p. 39; 1878, p. 31)
Thamnophilus punctatus (Shaw) — Müller (1847, p. 39; 1878, p. 31)
Hypocnemis cantator (Boddaert) — Müller (1847, p. 39; 1878, p. 32)
Chamaeza brevicauda (Vieillot) — Müller (1847, p. 40; 1878, p. 33)
Grallaria guatimalensis Prevost and Des Murs — Garrod (1877)
Conopophaga lineata (Wied) — Forbes (1881)
Conopophaga lineata (Wied) — Ames et al. (1968)
Conopophaga roberti Hellmayr — Ames et al. (1968)
Conopophaga aurita (Gmelin) — Müller (1847, p. 40; Pl. 6, fig. 12; 1878, p. 33)

Cartilaginous Elements.

The cartilages of this group are summarized in Table 2. A detailed description of each genus is beyond the scope of this paper, but the following generalizations may be made:

1) Dorsal and ventral Membranae tracheales are present in all genera. There are two types of Membranae, long and short.
   a) Among the genera examined by me, the long type is found only in *Formicarius, Chamaeza,* and *Grallaria.* The anterior limit of the Membrana is characterized by a gradual transition from narrow to broad elements, the inter-element membranes being successively narrower. In the three genera above only the dorsal Membrana is long, the ventral one being abruptly limited anteriorly.
   b) The short type of Membrana, found in all of the other genera studied, is characterized by an abrupt anterior limit, usually at about A-10. In this case the limiting element often has approximately the same width as all of the elements anterior to it. The element just posterior to the anterior limit is usually the narrowest of those crossing the Membrana.
2) Processi vocales are present in all genera, but are usually small and attached only to those elements within the limits of the Membranae tracheales (see *Taraba,* Pl. 3). Exceptions are the Processi of *Formicarius* (Pl. 3), *Chamaeza* (Pl. 4), *Conopophaga* (Pl. 4) and *Grallaria,* which are broad, thick and long, extending from A-1 or A-2 anteriad in *Formicarius* to A-10, in the various species of *Grallaria* to A-10, A-11 or A-12, in *Chamaeza* to A-17, and in *Conopophaga* to A-9, A-10, A-11 or A-12.
3) The pessulus is absent in all antbirds examined by me or by previous authors.
4) No forms are known possessing internal cartilages.
5) The configuration of the lower A-elements varies among the genera examined (see Table 2). In all specimens A-1 is divided and A-4 complete, the variability being limited to A-2 and A-3. The differences between A- and B-elements are less pronounced in this family than in others of the Furnarioidea. All of the B-elements are divided. Some are partly ossified and in many the plane of curvature is nearly perpendicular to the bronchial axis.

Musculature.

In syringeal musculature the family is sharply divided into two categories, which may be summarized as follows:

1) *Formicarius* (Pl. 3), *Chamaeza* (Pl. 4), *Grallaria* and *Conopophaga* (Pl. 4). M. tracheolateralis is variable in this group. In *Formicarius, Grallaria* and *Conopophaga* it is a narrow lateral band; in *Chamaeza* a broad ventrilateral one. Insertion in *Formicarius* and *Grallaria* is entirely on the anterior end of the Processus vocalis, except in YPM 1068 (*G. perspicillata*), in which the ventral fifth of the muscle inserts on A-10. In *Chamaeza* the ventral three-quarters of the fibers are attached to A-16 through A-18 and the lateral quarter of them to the Processus. In *Conopophaga* the fibers at the dorsal and ventral edges insert on A-10, A-11 and A-12, the remainder usually being continuous with M. sternotrachealis. In individuals with long Processi, the deep fibers insert on the anterior end of the Processus.

   In *Formicarius, Chamaeza* and *Grallaria,* M. sternotrachealis inserts wholly on the anterior end of the Processus, except in YPM 1068, in which the anterior fibers of M. sternotrachealis are continuous with the super-

TABLE 2. Configuration of the syringeal cartilages in the Formicariidae.

Genus	A-1	A-2	A-3	A-4	*Membranae tracheales* ventral	*Membranae tracheales* dorsal	*Processi vocales* attached to:
Cymbilaemus	div.	div.	i.d.	compl.	A-3 - A-9	A-4 - A-10	A-4 - A-9
Hypoedaleus	div.	div.	i.d.	comp.	A-3 - A-9	A-4 - A-9	A-4 - A-8
Taraba	div.	div.	comp.	comp.	A-2 - A-10	A-3 - A-11	A-2 - A-8
Sakesphorus	div.	div.	comp.	comp.	A-3 - A-9	A-3 - A-12	A-3 - A-4
Thamnophilus							
caerulescens	div.	i.d.	comp.	comp.	A-3 - A-9	same	A-5 - A-9
doliatus	div.	div.	comp.	comp.	A-3 - A-9	same	A-4 - A-8
punctatus	div.	div.	i.d.	comp.	A-3 - A-9	same	A-5 - A-8
Pygiptila	div.	div.	comp.	comp.	A-3 - A-12	same	A-6 - A-9
Dysithamnus	div.	comp.	comp.	comp.	A-2 - A-9	A-2 - A-10	A-2 - A-7
Thamnomanes	div.	i.d.	comp.	comp.	A-3 - A-9	A-1 - A-9	A-2 - A-8
Myrmotherula	div.	div.	comp.	comp.	A-3 - A-8	A-3 - A-9	A-4 - A-6
Herpsilochmas	div.	div.	i.d.	comp.	A-3 - A-10	A-2 - A-12	A-3 - A-8
Microrhopias	div.	div.	comp.	comp.	A-5 - A-10	A-3 - A-8	A-4 - A-8
Neorhopias	div.	i.d.	comp.	comp.	A-2 - A-9	A-4 - A-9	A-4 - A-6
	(div. A-2aR present)						
Drymophila	div.	div.	i.d.	comp.	A-3 - A-9	same	A-5 - A-8
Cercomacra	div.	comp.	comp.	comp.	A-2 - A-9	same	A-3 - A-9
Pyriglena	div.	div.	i.d.	comp.	A-3 - A-11	A-4 - A-12	A-4 - A-9
Hypocnemis	div.	comp.	comp.	comp.	A-4 - A-12	A-3 - A-12	A-4 - A-8
Hypocnemoides	div.	div.	comp.	comp.	A-3 - A-11	same	A-4 - A-7
Myrmeciza	div.	div.	comp.	comp.	A-2 - A-12	A-3 - A-10	A-6 - A-10
Myrmoderus	div.	div.	comp.	comp.	A-4 - A-9	A-3 - A-7	A-4 - A-7
Formicarius	div.	div.	div.	comp.	A-4 - A-10	A-3 - A-11	A- - A-
Chamaeza	div.	div.	i.d.	comp.	A-2 - about A-30*	A-2 - about A-21*	A-2 - A-14
Pithys	div.	div.	i.d.	comp.	A-4 - A-11	A-4 - A-10	A-4 - A-7
Gymnopithys	div.	div.	comp.	comp.	A-2 - A-9	A-2 - A-10	A-4 - A-7
Hylophylax	div.	div.	comp.	comp.	A-4 - A-10	A-3 - A-9	A-4 - A-7
Grallaria	div.	div.	comp.	comp.	A-3 - about A-30*	A-3 - about A-20*	A-4 - A-7
Conopophaga	div.	div.	i.d.	comp.	A-3 - A-11	A-2 - A-13	

*There is no finite anterior limit to the Membranae tracheales in *Chamaeza* and *Grallaria*.

ficial lateral fibers of M. tracheolateralis. In most specimens of *Conopophaga*. M. sternotrachealis is largely continuous with M. tracheolateralis, the deeper fibers inserting on A-10, A-11 and A-12. When the Processus is long the deeper fibers of M. sternotrachealis insert on its anterior end.

There are no intrinsic muscles in any of these genera.

Müller's descriptions of *Chamaeza* and *Conopophaga*, and Garrod's of *Grallaria* agree with the above regarding insertions of the extrinsic muscles and the lack of intrinsic ones. Forbes' description of *Conopophaga* applies only to individuals with short Processi.

2) All other genera of this family examined by me (example: *Taraba*, Pl. 3). M. tracheolateralis inserts ventrally and ventrilaterally on several elements anterior to the Membranae tracheales and sometimes also on the dorsal side of the anterior end of the Processus. M. sternotrachealis characteristically divides into two fasciculi. The posterior one inserts on the anterior end of the Processus, the anterior one on the dorsolateral surfaces of several elements immediately anterior to the Membrana. In some individuals there is fiber continuity between portions of the two extrinsic muscles. The paired intrinsic muscle, which I tentatively call M. vocalis ventralis, originates on the ventral surfaces of several elements immediately anterior to the Membrana. Usually the line of origin is most posteriorly situated near the ventral midline and angles anterolaterally, following the line of insertion of M. tracheolateralis. Extending across the anterior corner of the Membrana, M. vocalis ventralis inserts on the anterior end of the Processus immediately anterior to the insertion of M. sternotrachealis. The precise regions of origin and insertion of the intrinsic muscle vary greatly among the members of this diverse family. Usually the muscle extends between the two fasciculi of M. sternotrachealis.

Most of the characteristics of this second group were noted by Müller in his detailed descriptions of *Hypoedaleus* and *Thamnophilus*.

FAMILY CONOPOPHAGIDAE. ANTPIPITS AND GNATEATERS.

This family was erected by Forbes (1881) for the genera *Conopophaga* and *Corythopis*, on the basis of characters of the syrinx, sternum and tarsus. Ames et al. (1968) reexamined these and other characters in the two genera and compared them with a number of other suboscines, concluding that *Corythopis* must be placed in the superfamily Tyrannoidea and *Conopophaga* returned to the Formicariidae. The reader will find *Conopophaga* at the end of the Formicariidae (p. 26) and *Corythopis* in the subfamily Euscarthminae of the Tyrannidae (p. 66).

FAMILY RHINOCRYPTIDAE. TAPACULOS.

Specimens Examined.

Of 38 species in 12 genera (including *Melanopareia* Reichenbach[1] and *Psilo-*

[1]The genus *Melanopareia* was placed by Hellmayr (1924) in the Formicariidae, but W. W. Miller (*in* Wetmore, 1926) found that its metasternum has two pairs of notches, suggesting that the genus belongs in the Rhinocryptidae. Peters (1948) agreed with Wetmore and is followed here.

rhamphus Sclater[1]), I have examined the following 10 individuals in eight species and seven genera:

Pteroptochos tarnii (King), two specimens
Pteroptochos megapodius Kittlitz
Scelorchilus rubecula (Kittlitz)
Rhinocrypta lanceolata (Geoff. Saint Hilaire), two specimens
Teledromas fuscus (Scl. and Salv.)
Melanopareia maximilliani (D'Orbigny)
Scytalopus magellanicus (Gmelin)
Triptorhinus [= *Eugralla*] *paradoxus* (Kittlitz)

I know of only the following descriptions by previous authors:

Pteroptochos megapodius Kittlitz — Garrod (1877)
Scytalopus indigoticus (Wied) — Müller (1847, p. 41; 1878, p. 33)
Psilorhamphus guttatus (Menetries) — Plótnick (1958)

Cartilaginous elements.

Pteroptochos (Pl. 4) is typical of the family. A-1 and A-2 are divided; A-3 is incomplete dorsally; A-4 and subsequent elements are complete. Membranae tracheales are present ventrally and dorsally. The ventral one is limited posteriorly by A-3. Anteriorly the elements become successively wider, attaining a uniform width at about A-27 in *P. megapodius* and about A-20 in *P. tarnii*. The dorsal Membrana is limited abruptly by A-2 posteriorly and by A-14 anteriorly. There are prominent Processi vocales, attached at their broad bases to A-1 and A-2. They are narrow in the region of A-5 through A-9 and broad anteriorly, providing surfaces for muscle attachments. There are neither a pessulus nor internal cartilages.

Garrod's description of *P. megapodius* differed from the above only on minor points. He noted that elements A-3 through A-14, which crossed the Membranae as narrow bands, were incomplete laterally, "as they are in all the Trachaeophonae." In the latter remark Garrod was in error. Whatever the condition in his specimen, the elements crossing the Membranae are usually complete laterally. Removal of the Processi frequently damages the underlying elements, to which the Processi are attached.

Rhinocrypta is like *Pteroptochos*, differing as follows. A-1 is extremely heavy, about twice the width and thickness of elements anterior to the Membranae. A-2 is incomplete dorsally. A-1, A-2, and A-3 are joined ventrally by two narrow medial plates. At the anterior edge of the ventral Membrana A-16 and A-17 are incomplete ventrally and are intermediate in width between A-15 (the narrowest element) and A-18 (as wide as those anterior to it).

Teledromas is like *Pteroptochos*, differing as follows. Both Membranae are abruptly limited anteriorly by A-14. The trachea is very broad in the region of A-10 and strongly compressed dorsoventrally. The Processi are robust and extend from A-1 and A-2, to which they are fused, anteriorly to the level of A-13.

Scelorchilus is like *Pteroptochos*, differing as follows. A-3 is complete. The ventral Membrana ends abruptly at A-18 and the dorsal one at A-16.

[1]*Psilorhamphus* is included in this family, following Plótnick (1958).

Scytalopus is like *Pteroptochos*, differing as follows. A-3 is divided. Both Membranae are limited anteriorly by A-10, which is intermediate in width between A-9 and A-11 dorsally, but has the full width of A-11 ventrally. The Processi vocales are attached to A-2 and A-3 only. Müller's description agrees closely with the above.

Triptorhinus is like *Pteroptochos*, differing as follows. A-3 is complete. The dorsal Membrana is sharply limited by A-1 posteriorly and by A-13 anteriorly, the ventral one by A-2 and A-11. In other words A-2, A-11, and A-12 are narrow dorsally and broad ventrally.

Melanopareia (Pl. 4) is unlike all of the above in several ways. A-1 is divided; A-2 is incomplete dorsally; A-3 and subsequent elements are complete. The anterior limits of both Membranae are gradual, A-8 and A-9 being intermediate in width between A-7 and A-10. A rigid drum is formed by the fusion of A-10 through A-12 and, dorsally, through A-14. The Processi vocales are broad plates without constrictions. They are attached by fibrous connective tissue to A-2 through A-7. The maximum width of the trachea, at A-7, is about twice that where the width is uniform, anterior to A-14.

In describing the syrinx of *Psilorhamphus*, Plótnick did not mention details of the cartilages, but it appears from his illustration (showing only the dorsal view) that A-1 and A-2 are divided or incomplete dorsally. The dorsal Membrana evidently is rather short, being limited by A-2 and A-10.

Musculature.

In *Pteroptochos* (Pl. 4) M. tracheolateralis extends down the lateral surface of the trachea to insert on the anterior end of the Processus vocalis, with a few ventral fibers attached to A-16. M. sternotrachealis also inserts on the Processus, immediately posterior to M. tracheolateralis and partly surrounded by it. A thin, narrow intrinsic muscle, for which I tentatively use the name M. vocalis dorsalis, originates on A-16 adjacent to the dorsal fibers of M. tracheolateralis and spirals posteroventrally across the surface of the latter muscle to insert on the Processus just ventral to the insertion of M. tracheolateralis. The intrinsic muscle is more strongly developed in *P. tarnii* than in *P. megapodius*.

Garrod's description of *P. megapodius* was almost entirely devoted to cartilaginous elements. He mentioned the insertions of M. sternotrachealis and M. tracheolateralis on the Processus, but neither described nor illustrated an intrinsic muscle.

Scelorchilus is like *Pteroptochos*, differing as follows. M. tracheolateralis divides into two fasciculi at the level of A-19. The fasciculi insert on the anterior end of the Processus on either side of the insertion of M. sternotrachealis. The latter also divides into two fasciculi near its insertion: a dorsolateral one inserting on the Processus vocalis and on the lateral surfaces of A-16 through A-18 and a ventral fasciculus which inserts on the ventrilateral surfaces of A-16 through A-18 adjacent to M. tracheolateralis. M. vocalis dorsalis originates on the dorsolateral surfaces of A-13 through A-17 and extends superficial to the two extrinsic muscles to insert on the ventral edge of the Processus.

Triptorhinus is like *Pteroptochos*, differing as follows. M. tracheolateralis inserts along a spiral line from the lateral region of A-13 to the dorsolateral region of A-19. A narrow ventral fasciculus inserts on the ventrilateral surfaces of A-13 and A-14.

M. vocalis dorsalis originates on the dorsal surfaces of A-14 through A-23 and spirals posterolaterally to insert on the Processus vocalis.

Melanopareia (Pl. 4) is like *Pteroptochos,* differing as follows. M. tracheolateralis inserts on the ventral side of the Processus vocalis adjacent to the insertion of M. sternotrachealis. M. vocalis dorsalis originates on the dorsal surfaces of A-10 through A-12. Its insertion covers most of the ventrilateral surface of the Processus, from A-3 to A-6, where it is in contact with the insertion of M. tracheolateralis.

Rhinocrypta is like *Pteroptochos,* differing as follows. M. tracheolateralis divides into two fasciculi, a narrow dorsal one inserting on A-16 and a broad ventral one inserting on A-19 and A-20. M. vocalis dorsalis originates on the dorsolateral surfaces of A-17 through A-22. Its fibers are parallel to those of the ventral branch of M. tracheolateralis. The insertion is on the Processus, ventrally adjacent to the insertion of M. sternotrachealis.

Scytalopus is unlike all of the above. M. tracheolateralis inserts dorsolaterally in a broad area of A-11 and A-12 and laterally on the Processus vocalis. Some superficial dorsolateral fibers are continuous with part of M. sternotrachealis, the remainder of which inserts on the Processus. The intrinsic muscle consists of a narrow band of fibers nearly covered by M. tracheolateralis. It originates on the lateral surface of A-19 and inserts on the anterior end of the Processus. Without more specimens I am unwilling to name this muscle in the terms applied to those of other rhinocryptids. Müller mentioned the insertion of M. sternotrachealis on the Processus and stated without further description that the Processus is drawn upward by "other muscles."

Teledromas is unlike all of the above. M. tracheolateralis is a narrow lateral band inserting on the anterior end of the Processus vocalis. M. sternotrachealis inserts in a circular area of the Processus, immediately posterior to the insertion of M. tracheolateralis. There are no intrinsic muscles.

In *Psilorhamphus* Plótnick found one pair of intrinsic muscles, which he described as extensions of the Mm. tracheolaterales, "as in many birds." It is evident from the illustration that both the intrinsic muscle and M. tracheolateralis insert on the anterior end of the Processus, but I cannot make out whether the intrinsic muscle lies posterior or ventral to the extrinsic one. The origins of the muscles are not shown. M. sternotrachealis (called "costo-tracheal" by Plótnick) inserts directly on the anterior end of the Processus.

Superfamily Tyrannoidea.

NOMENCLATURE.

The nomenclature on p. 14 is applicable to this suborder, with the following additions:

1) Cartilaginous elements.

Internal cartilages. This term was applied by Miskimen (1963) to the paired cartilaginous plates lying in the internal tympaniform membranes. Müller's (1847) term *Cartilago arytenoidea* implies homology to the arytenoid cartilages of the mammalian larynx and hence is not appropriate. Internal cartilages are variable in shape and in number and may float freely in the membranes or be attached to other elements.

2) Muscles.

M. obliquus ventralis is a new name for the paired intrinsic muscle originating directly or on a median raphe at or near the ventral midline. It extends posterolaterally, to insert on one or more elements or on the membranes between them. This muscle was first named by Miskimen (1963), but the name that she used, "M. syringeoventralis", is much like the name "M. syringeus ventralis," applied by Setterwall (1901) and others to one of the oscine syringeal muscles. To avoid misunderstanding a wholly new name appears justified. Müller applied the term "kehlkopfmuskel" to this and all other intrinsic syringeal muscles.

M. obliquus lateralis is a new name for another paired intrinsic muscle that originates on the lateral surface of one or more A-elements and extends posteriorly or posteroventrally to insert on one or more elements, usually near the insertion of M. obliquus ventralis. Miskimen (1963) called this "M. syringeo-lateralis."

M. obliquus dorsalis originates on or near the dorsal midline and extends posterolaterally to insert on one or more A- or B-elements. It has not been described by previous authors.

FAMILY COTINGIDAE. COTINGAS.

Specimens Examined.

Of 92 species in 34 genera (including *Pseudattila* Zimmer 1936, *Zaratornis* Koepke 1954, and *Conioptilon* Lowery and O'Neill 1966), I have examined the following 39 individuals of 30 species in 23 genera:

Phoenicircus carnifex (Linnaeus)
Heliochera rubrocristata (Lafr. and D'Orb.)
Cotinga amabilis Gould
Cotinga maculata (Müller)
Xipholena punicea (Pallas)
Carpodectes nitidus Salvin
Euchlornis jucunda (Sclater)
Euchlornis aureopectus (Lafresnaye), two specimens.
Iodopleura isabellae (Shaw and Nodder)
Attila spadiceus (Gmelin)
Attila cinnamomeus (Gmelin)
Casiornis rufa Vieillot
Laniocera rufescens (Sclater)

Rhytipterna holerythra (Scl. and Salv.), three specimens.
Lipaugus unirufus Sclater
Pachyramphus rufus (Boddaert)
Pachyramphus polychopterus (Vieillot), two specimens
Pachyramphus viridis (Vieillot)
Platypsaris aglaiae (Lafresnaye), three specimens
Tityra semifasciata (Spix)
Tityra inquisitor (Lichtenstein)
Tityra cayana (Linnaeus)
Querula purpurata (Müller)
Pyroderus scutatus (Shaw), two specimens
Cephalopterus ornatus Geoff. Saint Hilaire
Perissocephalus tricolor (Müller)
Gymnoderus foetidus (Linnaeus)
Conioptilon mcilhennyi Lowery and O'Neill
Procnias tricarunculata (J. and E. Verreaux)
Rupicola rupicola (Linnaeus), three specimens

I know of the following descriptions by previous authors:

Phibalura flavirostris Vieillot — Müller (1847, p. 32; 1878, p. 26)
Xipholena punicea (Pallas) — Müller (1847, p. 31; Pl. 6, figs. 1, 2; 1878, p. 26)
Iodopleura pipra (Lesson) — Müller (1847, p. 30; 1878, p. 25)
Calyptura cristata (Vieillot) — Müller (1847, p. 30; 1878, p. 25)
Lipaugus cineraceus (Vieillot) — Garrod (1877b)
Pachyramphus rufus (Boddaert) — Müller (1847, p. 32; Pl. 6, fig. 6; 1878, p. 26)
Platypsaris aglaiae (Lafresnaye) — Garrod (1877b)
Tityra cayana (Linnaeus) — Müller (1847, p. 31; Pl. 6, fig. 5; 1878, p. 26)
Pyroderus scutatus (Shaw) — Garrod (1878)
Cephalopterus ornatus Geoff. Saint Hilaire — Tschudi (1843)
Cephalopterus ornatus Geoff. Saint Hilaire — Sick (1954)
Perissocephalus tricolor (Müller) — Müller (1847, p. 31; Pl. 6, fig. 4; 1878, p.26)
Conioptilon mcilhennyi Lowery and O'Neill — Lowery and O'Neill (1966)
Procnias alba (Hermann) — Müller (1847, p. 26; Pl. 1, figs. 1-6; 1878, p. 22)
Procnias nudicollis (Vieillot) — Müller (1847, p. 27; Pl. 1, figs. 8-14; 1878, p. 23)
Rupicola rupicola (Linnaeus) — Müller (1847, p. 31; Pl. 6, fig. 3; 1878, p. 26)

Cartilaginous Elements.

In *Cotinga* (Pls. 15 and 16) A-1 is divided; A-2 is double; A-3 is divided; A-4 is incomplete ventrally; A-5 and subsequent elements are complete. Each element has a thin flange at its posterior edge overlapping the anterior edge of the next element. The pessulus is fused to A-4 at the dorsal midline. At its ventral end it is connected to A-3 and A-4 by cartilaginous strips. There are no internal cartilages. All of the B-elements are divided. The middle third of B-1 is enclosed in a mass of fibrous connective tissue, some of which is attached to A-1 and B-2.

Xipholena is like *Cotinga,* differing as follows. A-1 through A-4 are divided. The pessulus is fused dorsally to both A-4 and A-5 and ventrally to A-5. There is no fibrous connective tissue enclosing B-1. Müller's description and illustration of *Xipholena* agree closely with the above.

Conioptilon is like *Cotinga,* differing as follows. A-1 through A-4 are divided and there is an extra component, A-3aL. The elements lack the flanges found in *Cotinga.* The pessulus is fused to A-4 at both ends. B-1 is only slightly curved and is not enclosed in connective tissue. Lowery and O'Neill (1966), whose information was provided by me from the specimen described here, were concerned only with the general similarity of the syrinx of *Conioptilon* to those of the Cotinginae and Gymnoderinae.

Phoenicircus is like *Cotinga,* differing as follows. A-1 through A-4 are divided. A-1 is ossified only for the dorsal quarter, but this may be individually variable. The element is quite narrow and is straighter than A-2. The pessulus ends dorsally in a small plate which lies between the ends of A-3 and A-4. At the ventral end it butts with the ends of A-3. The ventral ends of A-3 and A-4 are tightly bound together with fibrous connective tissue. There is no mass of tissue surrounding B-1.

Euchlornis is like *Cotinga,* differing as follows. The two species examined differ slightly from each other. In *E. jucunda* A-1 through A-5 are divided; A-6 and subsequent elements are complete. The pessulus is fused to A-6. In *E. aureopectus* only A-1 through A-3 are divided; A-4 and subsequent elements are complete. The pessulus is fused to A-4 at both ends. In both species B-1 is a very heavy element, bent anteriad at the ends.

Tityra is like *Cotinga,* differing as follows. There are minor variations among the specimens examined. In *T. semifasciata* A-3 is complete and carries the pessulus. There is an extra divided component A-2aR. In *T. inquisitor* A-3 is divided and fused dorsally to A-4, which is complete and bears the pessulus. In *T. cayana* A-1 through A-5 are divided and the pessulus is absent. In all three specimens the anterior ends of the internal tympaniform membranes consist of a continuous sheet of cartilage which is attached to the dorsal and ventral ends of the divided elements, and contains the pessulus. At its edges the sheet blends into connective tissue, which encloses the ends of B-1. Müller's specimen of *T. cayana* was virtually identical to mine, to judge from his illustration.

Heliochera is like *Cotinga,* differing as follows. Only A-1 is divided; A-2 and subsequent elements are complete. The pessulus is fused dorsally and ventrally to A-2. Partial dissection by C. William Beebe has removed the connective tissue surrounding B-1, if any was present.

Of *Phibalura,* Müller (1878, p. 26) stated only that "the thin lateral muscle is inserted into the third bronchial ring," suggesting that probably only the lower two or three A-elements were divided. He described *Calyptura* as like "the true Ampelinae" (Cotinginae) and we may infer from the description that A-1 and possibly A-2 are divided.

Querula is unlike all of the above. The specimen is lacking everything posterior to B-1. A-1 through A-4 are divided and are very broad, each element overlapping the one posterior to it. A-5 is incomplete dorsally; A-6 and subsequent elements are complete. B-1 is divided and narrow. A narrow pessulus is fused to A-6 at both ends. The entire region from A-1 through A-6 consists of a hemispherical chamber, the diameter of which is about twice that of the trachea at A-10.

Carpodectes is like *Querula,* differing as follows. A-1 through A-7 are divided; A-8 and subsequent elements are complete. The ventral ends of B-1 through A-7 are connected by a horseshoe-shaped piece of soft cartilage, the ends of which almost touch at B-1. A similar cartilage joins the dorsal ends of the same elements. The narrow pessulus is fused to A-8 at both ends.

Pyroderus is unlike all of the above (see Pl. 20). Immediately behind the larynx the trachea is enlarged, mostly dorsoventrally, forming a long chamber, elliptical in cross section. In the region of A-21 through A-26 the trachea tapers to a circular cross section. A second chamber lies in the region of bifurcation, enclosed by B-1 through A-6. It is more conical in shape than hemispherical. The lateral diameter of the syrinx at A-1 is about three times that at A-10, where the lower trachea is narrowest. A-1 and A-2 are divided; A-3 is incomplete dorsally; A-4 and subsequent elements are complete. A-4 and A-5 are broadly fused at the dorsal and ventral midlines, as are A-5 and A-6. A-3 and A-4 are fused at the ventral midline only. The broad, heavy pessulus is fused to A-3 at the ventral end only. The posterior ventral edge of A-3 has a deep semicircular indentation on each side of the midline and the anterior ventrilateral edge of A-2 has similar indentations. The two combine to create a pair of roughly circular membranous windows completely bordered by the elements, which are tightly attached to each other by fibrous connective tissue at the edges of the windows. The posterior lateral edge of A-1 has a shelf-like extension projecting well beyond B-1. There are only six B-elements, all of them divided. They decrease in size progressively in the posterior direction, resulting in strongly tapered bronchi. Garrod's description and illustrations of the syrinx of *Pyroderus* agree closely with the above.

Perissocephalus is like *Pyroderus,* differing as follows. A-1 through A-4 are divided; A-5 and subsequent elements are complete. The dorsal and ventral fifths of each divided element are soft cartilage, while the middle three-fifths is hard. The soft regions are convex, relative to the lumen. A small semicircular piece of soft cartilage connects the ends of A-1 through A-4, also touching B-1. The lower A-elements in this genus and in those below lack the elaborate sculpturing found in *Pyroderus.*

Müller's description of *Perissocephalus* implied that it is much like *Pyroderus.* He mentioned that A-1 through A-5 are divided and that there is an enlargement of the anterior part of the trachea as in *Cephalopterus.*

Cephalopterus is like *Pyroderus,* differing as follows. A-1 through A-5 are divided; A-6 and subsequent elements are complete. The pessulus (Pl. 21) is fused to A-6 at both ends and is indented to receive the ends of A-5, which fit closely to it. At each midline, where the pessulus meets A-6, there is a triangular hole with the point directed anteriad. There are only four B-elements. They are delicate and successively smaller in diameter. The descriptions of *Cephalopterus* by Tschudi and by Sick were confined to the exterior shapes of the respiratory tubes. Both noted the anterior expansion of the trachea, the chamber in the syringeal region, and the short bronchi.

Gymnoderus is like *Pyroderus,* differing as follows. The trachea is expanded in the region of A-8 through A-19, rather than more anteriorly. The dorsoventral diameter at A-13 is about twice the lateral diameter; at A-5 the ratio of the two diameters is about 1.5 to 1. A-1 through A-3, all divided elements, are arched, concave posteriorly. The pessulus is fused to A-4 at both ends. There are six B-elements, B-1 being heavy and dorsally spatulate, the others being delicate and decreasing in diameter consecutively.

Rupicola is unlike all of the above. A-1 through A-3 are divided; A-4 and subsequent elements are complete. A-4 through A-6 are wholly fused, except for ventrilateral spaces between A-5 and A-6 in the AMNH specimen. The pessulus is fused to A-4 at both ends. B-1 is closely fitted to A-1 from which it differs in shape and hardness. The NYZS specimen was stained with alizarin by Dr. Beebe (using the technique of

Hollister, 1934) in order to determine the degree of calcification of the elements. All of the A-elements were heavily stained, the B-elements virtually not at all. Müller mentioned only the musculature of *Rupicola.*

Procnias is unlike all of the above. A-1 through A-4 are divided and are fused, forming a pair of broad curved plates. The diameter of the syrinx at A-1 is about three times that at A-7. A-5 is a very narrow complete element, the edges of which are closely fitted to adjacent elements. The pessulus appears to float in about the middle of the long space between A-1 and B-1, held in place by the surrounding membranes. The A-1/B-1 membrane is very long anteroposteriorly, about equal to the distance covered by the first six A-elements.

Müller's detailed descriptions of *P. alba* and *P. nudicollis* were primarily concerned with musculature. In the former species he found two divided elements (probably A-1 and A-2) anterior to the long membrane; in the latter species there was only a single divided element there. Possibly the "single" element was composed of several fused elements.

Attila (Pls. 15 and 16) is unlike all of the above. A-1 is divided; A-2 is double; A-3 is divided; A-4 is incomplete dorsally; A-5 and subsequent elements are complete. In YPM 2130 there is an extra divided component, A-3aR. B-1 is heavy and is spatulate dorsally. The pessulus is attached to A-4 ventrally and free dorsally. There are two pairs of internal cartilages. A large ⅃-shaped dorsal pair is fused anteriorly to the medial region of A-2, the short arm of each "⅃" extending ventrad. The other pair float in the ventral part of the internal tympaniform membranes at the level of B-2. Each is a small "⅃" with the corner situated anteriorly and the short arm directed dorsad. The bronchi are long and straight, with very little taper.

Casiornis is like *Attila,* differing as follows. A-3 is incomplete ventrally and A-4 is complete. The pessulus is a soft narrow bar fused dorsally to A-3 and free ventrally. The internal cartilages are more J-shaped than ⅃-shaped, and are about half as wide as in *Attila.* The smaller pair are short straight bars in line with the ventral ends of the larger ones.

Rhytipterna is like *Attila,* differing as follows. The pessulus ends ventrally in a small elliptical plate which fits the space between the ventral ends of A-2 and A-3 but is not fused. The dorsal internal cartilages are much narrower than those of *Attila* and are strongly J-shaped. The ventral pair are small thick bars close to the ventral ends of the dorsal pair.

Laniocera is like *Attila,* differing as follows. A-2 is divided and A-3 is complete. The two elements are fused near the ventral midline. The ventral internal cartilages are short, straight thick bars, flattened on their medial surfaces, where they are in contact with each other.

Iodopleura is unlike all of the above. A-1 is divided; A-2 is incomplete dorsally; A-3 and subsequent elements are complete. The midventral region of A-2 is very broad and blends imperceptibly into the pessulus, which touches the dorsal ends of A-2 but is not fused to them. A pair of very small, short, roughly triangular internal cartilages is fused to the pessulus near the ends of A-2. All of the B-elements are divided. B-1 is shorter and straighter than the others, resulting in markedly constricted bronchi. The latter are long and nearly untapered.

Pachyramphus is unlike all of the above. In *P. rufus* and *P. polychopterus* A-1 is divided; A-2 is incomplete ventrally; A-3 and subsequent elements are complete. There

is no flare in the syringeal region, A-1 having about the same diameter as the more anterior elements. In both specimens of *P. polychopterus* the pessulus is fused dorsally to A-2 and is free ventrally; in the specimen of *P. rufus* it is fused ventrally to A-2R; and in *P. viridis* A-2 is complete and bears the pessulus. There is a single pair of very small, straight, narrow, internal cartilages, situated at the dorsal edge of the internal tympaniform membranes. Müller's description of *P. rufus* was concerned only with the musculature.

Platypsaris is like *Pachyramphus,* differing only in that A-2 is divided and the internal cartilages are slightly wider. The pessulus is attached to A-3. Garrod apparently found A-2 to be complete in his specimen. His description does not make clear the position of the A-1/B-1 membrane, for he mentioned (1878, p. 143) the "the second bronchial semi-ring is not modified" (in comparison with the first semi-ring, which is "of the same flattened and deep nature as the tracheal rings"), but that the third semi-ring is "the commencement of the normal bronchus."

Lipaugus is unlike all of the above. A-1 and A-2 are divided; A-3 are subsequent elements are complete. A-2 through A-4 are connected by areas of soft cartilage, creating a semi-rigid drum. The pessulus is fused to A-3 at both ends. The 15 B-elements are of nearly uniform size, resulting in long, straight, only slightly tapered bronchi. The middle three-fifths of each B-element is ossified. B-1 is arched anteriorly and lies close to A-1, with the intervening region filled with fibrous connective tissue. There are no internal cartilages. The syrinx of *L. cineraceus,* as described by Garrod, is identical to that of *L. unirufus.*

Musculature.

In *Cotinga* (Pls. 15 and 16), M. tracheolateralis is a narrow, lateral band which broadens near its insertion to nearly twice its anterior width. It inserts on the connective tissue surrounding B-1. In my specimen of *C. amabilis* a slip from the dorsal edge of the muscle inserts on the dorsolateral surface of A-7 (probably an individual variant). In both species M. sternotrachealis inserts on the dorsolateral surfaces of A-9 through A-14, adjacent to the dorsal edge of M. tracheolateralis. There are no intrinsic muscles.

Xipholena is like *Cotinga,* differing as follows. About the ventral third of the fibers of Mm. tracheolaterales are attached to the trachea at A-8 on the left and at A-9 on the right. The attachment is not readily apparent and seems to involve only the deep fibers of the muscle. M. sternotrachealis inserts on A-12 through A-14.

Euchlornis is like *Cotinga,* differing only in that M. tracheolateralis is proportionately twice as wide and M. sternotrachealis is continuous with the dorsal superficial fibers of M. tracheolateralis at A-15.

Heliochera is like *Cotinga,* differing only in that M. sternotrachealis inserts on A-15 and A-16.

Phibalura and *Calyptura* are like *Cotinga,* to judge from Müller's brief descriptions. He mentioned only that they have thin lateral Mm. tracheolaterales and no intrinsic muscles.

Rupicola is like *Cotinga,* differing only in that M. tracheolateralis is broad anteriorly, narrowing at the level of A-15 through A-20, and that M. sternotrachealis is continuous with the dorsal fibers of the lateral muscle. Müller described the "thin

lateral muscle" as inserting on "the first really small halfring" ["an den ersten schon schmalen Halbring," (Müller, 1847, p. 31) translated by Bell (Müller, 1878, p. 26) as "the first halfring, which is quite small"]. It is evident from his illustration that Müller did not mean "the first halfring," for he clearly showed the insertion on B-1, with A-1 divided.

Querula is like *Cotinga*, differing as follows. M. tracheolateralis inserts on A-1. M. sternotrachealis is continuous with the dorsal fibers of M. tracheolateralis, which it meets at A-10.

Carpodectes is like *Cotinga*, differing only in that M. tracheolateralis is proportionately half as wide and inserts on A-1; and M. sternotrachealis inserts directly on the lateral surfaces of A-10 through A-12.

Pyroderus is like *Cotinga*, differing as follows. M. tracheolateralis is attached to the center of B-1 by a broad tendon which is folded over the projecting edge of A-1. M. sternotrachealis meets the trachea at A-17 and inserts by a fan-shaped tendon to A-18 through A-23.

Perissocephalus is like *Cotinga*, differing as follows. M. tracheolateralis is free of the trachea from A-9 to A-2, being straight where the lateral surface of the syrinx is concave. M. sternotrachealis inserts on A-11 through A-14. Müller did not mention the muscles in his description of this genus.

Cephalopterus is like *Cotinga*, differing as follows. M. tracheolateralis inserts on the middle of A-1. M. sternotrachealis is continuous with the superficial ventral fibers of the lateral muscle. Tschudi stated that the lateral muscle in his specimen inserted on the fourth bronchial semiring, which was A-1 only if A-5 was complete.

Gymnoderus is like *Cotinga*, differing as follows. M. tracheolateralis bends ventrad in the region of A-20 and broadens so that each muscle covers about one-sixth of the tracheal circumference at A-13, where both the width of the muscle and the dorsoventral diameter of the trachea are greatest. The muscle then bends dorsad, tapering rapidly, and inserts in a narrow area near the dorsal end of B-1. M. sternotrachealis is extremely narrow (possibly an artifact of the age of the specimen) and is continuous with the dorsal superficial fibers of M. tracheolateralis.

Procnias is unlike all of the above. M. tracheolateralis is thick and narrow, inserting on the lateral surface of A-5. A thick pad of intrinsic muscle covers the syrinx, on all sides, from A-4 to B-2. It originates on A-1 through A-4 and extends posteriad to insert on the A-1/B-1 membrane, B-1, the B-1/B-2 membrane, and B-2. Some fibers extend around the dorsal ends of the elements to the medial surface of the internal tympaniform membranes. By far the largest part of the insertion is on the A-1/B-1 membrane, which is tough and fibrous. M. sternotrachealis inserts on the ventrilateral surface of the intrinsic muscle by a broad fan-shaped tendon. A particularly thick part of this tendon is attached to the posterior surface of the muscle. Müller's detailed descriptions and illustrations of *P. alba* and *P. nudicollis* agree closely with the above.

Attila (Pls. 15 and 16) is unlike all of the above. The Mm. tracheolaterales are broad ventrilateral bands for most of their length, each being about 60 degrees of the tracheal circumference wide. They broaden to touch each other at the ventral midline in the region of their insertion, on the ventral two-thirds of A-6. M. sternotrachealis inserts on the lateral surfaces of A-14 through A-16, adjacent to the dorsal edge of M. tracheolateralis. An intrinsic muscle, for which I tentatively employ the name

M. obliquus ventralis, originates adjacent to the ventral midline of A-4 through A-6 and ventrilaterally along A-6 and A-5. It extends laterad and posteriad to insert on the center of the A-1/B-1 membrane.

Casiornis is like *Attila,* differing as follows. The Mm. tracheolaterales meet ventrally at about A-18 and remain in contact to their insertion, on A-5. M. sternotrachealis inserts on A-9 through A-11. M. obliquus ventralis originates midventrally on A-3 through A-5 and laterally along A-5. Its insertion is mostly on A-1, with a few superficial fibers of the dorsal region attached to the A-1/B-1 membrane.

Laniocera is like *Attila,* differing as follows. The Mm. tracheolaterales meet ventrally high on the trachea and remain in contact to their insertion, on A-3 ventrally and on A-4 laterally. M. sternotrachealis inserts on the membranous sheath covering M. tracheolateralis, with a few dorsal fibers in continuity with the latter muscle. M. obliquus ventralis originates on A-3 ventrally and on A-4 ventrilaterally. At their ventral edges the pair overlap. The right muscle originates along the anterior edge of element A-3 on both sides of the midline and its fibers overlie those of the left muscle, which originates on the posterior edge of the element, also on both sides of the midline. They insert symmetrically on the respective A-1/B-1 membranes.

Iodopleura is like *Attila,* differing as follows. The Mm. tracheolaterales are very thin and completely cover the ventral two-thirds of the trachea, inserting on A-3. M. sternotrachealis inserts on the dorsolateral surfaces of A-5 through A-7, with a few fibers continuous with M. tracheolateralis. The intrinsic muscles, apparently Mm. obliqui ventrales, originate on A-3 adjacent to the insertion of the Mm. tracheolaterales and midventrally on the A-2/A-3 membrane. They insert directly on the dorsal ends of the respective halves of B-1. Müller found no intrinsic muscles in *Iodopleura pipra.*

Rhytipterna is like *Attila,* differing as follows. M. sternotrachealis is wholly continuous with the dorsal fibers of M. tracheolateralis. M. obliquus ventralis originates on the midventral region of A-3 and A-4 and ventrilaterally on A-4; it inserts on the ventral half of A-1.

Lipaugus is unlike all of the above. The Mm. tracheolaterales are wide, covering the ventral half of the trachea down to A-13, where they separate and narrow. Each inserts on the middle third of the respective half of B-1. M. sternotrachealis inserts directly on A-9 through A-15, passing through a slot in M. tracheolateralis. There appear to be intrinsic muscles in my specimen, but damage to the ventral region of the syrinx between A-4 and A-8 precludes accurate determination of the myology of that region. On each side is a band of muscle lying superficial to M. tracheolateralis and apparently originating on A-5 and A-6 just medial to the ventromedial edge of the latter muscle. This superficial layer extends obliquely across the extrinsic muscle to insert on B-1, just lateral to the insertion of M. tracheolateralis. Garrod found no intrinsic muscles in *L. cineraceus.*

Pachyramphus is unlike all of the above. The Mm. tracheolaterales converge at about A-35 and their combined mass becomes narrower and thicker toward the insertion. They terminate at A-3 on a single tendinous sheet which shortly divides into two narrow tendons. These are attached to the right and left ventral ends of A-1 and B-1. M. sternotrachealis is a robust muscle which inserts on the ventrilateral surfaces of A-7 through A-11. The exact area of insertion varies slightly among the five specimens. In YPM 1041 (*P. polychropterus*) it is on A-8 through A-10, in YPM 2577 (*P. viridis*) on A-9 through A-11. M. obliquus ventralis originates ventrilaterally

on A-3 and A-4, adjacent to M. tracheolateralis, and extends laterally and posteriorly to insert by a broad tendon to the middle of B-1.

In *P. rufus* Müller noted the ventral narrowing of the Mm. tracheolaterales but stated that they terminate at the end of the trachea (A-2); apparently he did not find a tendinous insertion. His description of the intrinsic muscle agrees generally with my findings.

Platypsaris is like *Pachyramphus,* differing as follows. M. tracheolateralis, although similar in shape to that of *Pachyramphus,* lacks the tendinous insertion; it inserts directly on the ventral end of A-1. M. sternotrachealis inserts on A-14 through A-17, with some fibers continuous with the dorsal fibers of M. tracheolateralis. The origin of M. obliquus ventralis includes A-2, as well as A-3 and A-4, and the insertion is atendinous, on the dorsal end of B-1.

In Garrod's description of *P. aglaiae* the positions of the individual muscles are difficult to ascertain. He mentioned that the "syringeal muscles" did not reach the second bronchial semiring (B-1) but he appears to have meant M. tracheolateralis. He stated that this species is identical to *Pachyramphus rufus* as described by Müller, but the illustration of *Platypsaris* shows no oblique intrinsic muscle as shown by Müller. In view of the wide disparity of both descriptions and illustrations it is odd that Garrod should have stressed the similarity of the two syringes.

FAMILY PIPRIDAE. MANAKINS.

Specimens Examined.

Of 56 species in 21 genera, I have examined the following 15 individuals of 11 species and seven genera:

Piprites chloris (Temminck)
Pipra mentalis Sclater, two specimens
Pipra erythrocephala (Linnaeus)
Chiroxiphia lanceolata (Wagler)
Chiroxiphia caudata (Shaw and Nodder), two specimens
Ilicura militaris Parzudaki
Corapipo leucorrhoa (Sclater)
Manacus vitellinus (Gould)
Manacus candei (Parzudaki)
Schiffornis virescens (Lafresnaye)
Schiffornis turdinus (Wied), three specimens

I know of the following descriptions by previous authors:

Pipra erythrocephala (Linnaeus) — Müller (1847, p. 30; Pl. 4, figs. 4, 5; 1878, p. 25)
Pipra pipra (Linnaeus) — Müller (1847, p. 29; Pl. 4, figs. 9-11; 1878, p. 24)
Chiroxiphia pareola (Linnaeus) — Müller (1847, p. 29; Pl. 4, figs. 6-8; 1878, p. 24)
Chiroxiphia pareola (Linnaeus) — Lowe (1942)
Manacus manacus (Linnaeus) — Müller (1847, p. 30; 1878, p. 25)
Manacus vitellinus (Gould) — Lowe (1942)
Schiffornis turdinus (Wied) — Garrod (1877b)

Cartilaginous Elements.

In *Piprites* A-1 through A-3 are divided; A-4 is incomplete dorsally, A-5 and subsequent elements are complete. The pessulus is narrow at its ventral end, where it is fused to A-4, and broad dorsally, where it is fused to A-3L and A-4R. The region between the pessulus and the dorsal ends of A-1, A-2, and A-3R is not membranous, but consists of a thin sheet of soft cartilage. Posteriorly the sheet is about twice as thick as the A-elements and has two short, pointed extensions, directed posteriad. There are no internal cartilages. The B-elements are all divided, B-1 being broad and spatulate at its dorsal end, the others being uniformly narrow.

Schiffornis is unlike *Piprites*. In *S. turdinus* A-1 and A-2 are divided; A-3 and subsequent elements are complete. The pessulus is fused to A-3 at both ends. B-1 is heavier than either the A-elements or the other B-elements and is nearly straight. The result of this straightness is a constriction of the air passages at B-1. A single pair of internal cartilages is attached to the dorsal ends of A-2. They are J-shaped with the curvature directed ventrad. *S. virescens* differs from *S. turdinus* only in that A-3 is incomplete dorsally and is fused to A-4 for its ventral half and at its dorsal end. The pessulus is fused dorsally to A-4. Garrod's description of *S. turdinus* agrees with the above in all major points.

Manacus is unlike both of the above. A-1 through A-4 are divided; A-5 and subsequent elements are complete. A-1 is about twice the width of the other A-elements and has a projection along its posterior edge, to which *M. tracheolateralis* is attached. A-2 is wholly fused to A-1 and to A-3 for its ventral half. The narrow pessulus is fused to the ventral ends of A-2, but is free dorsally. The dorsomedial region between the ends of A-2 and A-3 consists of a sheet of soft cartilage, thickened at its posterior edge. Müller's brief description of *M. manacus* was largely concerned with musculature, but he did state that the "third bronchial ring" (apparently A-1) was very strong. Lowe's remarks on *M. vitellinus* are in accord with the above.

Pipra is unlike all of the above. In *P. erythrocephala* A-1 is divided; A-2, A-3 and A-4 are double; A-5 is incomplete ventrally; A-6 and subsequent elements are complete. A-1 and A-2 are completely fused, as are A-5, A-6 and A-7, the last three forming a rigid drum. The B-elements are soft and quite delicate. B-1 and B-2 are fused into a single broad plate at their dorsal ends. There are no internal cartilages. The pessulus is a medial extension of the dorsal edge of A-5 and is in contact with A-4 for most of its length. It terminates ventrally in an oblong shield that overlies the midventral regions of A-2 through A-5. *P. pipra* differs only in that the drum is composed of A-5 and A-6.

Müller's description and illustration of *P. pipra* differs from the above only in minor points: in his specimen A-2 was divided and there apparently was no drum. In *P. erythrocephala* he found the cartilages to be like those of *P. pipra*.

Corapipo (Pls. 15 and 16) is unlike all of the above. A-1 through A-4 are divided; A-5 through A-7 are incomplete dorsally; A-8 and subsequent elements are complete. The narrow pessulus is fused to A-8 dorsally and to A-5 ventrally. The dorsal ends of A-1 through A-4 are connected by a pair of narrow bars of soft cartilage. There are no internal cartilages. There is a prominent projecting shelf in the middle of B-1 but no muscles are attached to it. The dorsal ends of B-1 and B-2 are spatulate and fused to each other.

Chiroxiphia (Pls. 15 and 16) is unlike all of the above. In *C. lanceolata* A-1 through A-3 are divided; A-4 and A-5 are incomplete dorsally; A-6 and subsequent elements are complete. A-6 through A-11 are fused into a drum, smooth dorsally but showing the fusion seams ventrally. A short mid-dorsal extension of A-6 lies in the dorsal openings of A-4 and A-5. The dorsomedial region from B-1 to A-4 consists of a single sheet of soft cartilage, attached to the dorsal ends of A-1 through A-4 and to the ventral ends of B-1 and A-1. The pessulus and internal cartilages are lacking. *C. caudata* differs from *C. lanceolata* in that A-6 and A-7 are incomplete dorsally and the drum consists of A-8 through A-14. In YPM 2587, A-7R is fused dorsally to the drum and in the AMNH specimen A-7L is fused dorsally to the drum.

Müller's description and illustration of *C. pareola* are similar to the above. He found A-1 through A-3 divided; A-4 through A-6 or A-7 incomplete dorsally; A-8 and subsequent elements complete. In the illustration about seven elements are shown as incomplete dorsally. No mention is made of a drum, and in the illustration only A-11 and A-12 are shown as fused.

Ilicura is unlike all of the above. A-1 through A-5 are divided; A-6 is incomplete dorsally; A-7 and subsequent A-elements are complete. The ventral ends of the divided elements are narrow and slightly spatulate. The dorsal ends of B-1 and A-1 through A-5 are connected by a bar of soft cartilage. The pessulus extends from A-2 ventrally to A-6 dorsally and is free at both ends. The difference between A-1 and B-1 is not as great as in most manakins, B-1 being close to and parallel to A-1, but different in consistency and cross section. The ventral ends of B-1 are almost completely fused. The bronchi are short and strongly tapered, there being only seven B-elements.

Musculature.

In *Piprites* the Mm. tracheolaterales are narrow lateral bands inserting directly on the center fifth of B-1. M. sternotrachealis is wholly continuous with the dorsal half of M. tracheolateralis, which it meets at the level of A-8. There are no intrinsic muscles.

Schiffornis is unlike *Piprites*. M. tracheolateralis is of medium width, occupying the lateral 60° of the trachea on each side. It inserts on A-4 through A-6 in *S. turdinus* and on A-3 through A-5 in *S. virescens*. M. sternotrachealis inserts directly on A-9 and A-10, dorsally adjacent to M. tracheolateralis. A short, broad intrinsic muscle originates immediately posterior to the insertion of M. tracheolaterales and extends posterodorsad to insert by a short tendon to the subterminal dorsal quarter of B-1. In one specimen of *S. turdinus* the intrinsic muscle is covered by a thin, but full-width extension of M. tracheolateralis, which inserts just beyond the intrinsic muscle.

In his description of *S. turdinus* Garrod mentioned only M. tracheolateralis, which he found to insert in the center of "the second bronchial semiring" (A-1). Apparently he did not find an intrinsic muscle.

Manacus is unlike all of the above. The Mm. tracheolaterales converge at the level of A-27 and thicken midventrally, resulting in a prominent bulge in the region of A-4 through A-7. The majority of the thick portion consists of the left muscle, the fibers of which lie down on both sides of the ventral midline, but insert only on the left. The insertion is along the ventral seven-eighths of A-1. M. sternotrachealis is continuous with the lateral superficial fibers of M. tracheolateralis, which it meets at

A-11. There is no intrinsic muscle. Müller's description of *M. manacus* and Lowe's of *M. vitellinus* agrees closely with the above description, which is based on *M. candei* and *M. vitellinus*. Lowe illustrated but did not describe a peculiar form of M. sternotrachealis in which the pair of muscles share a midventral tendon with diffuse attachment. I have not found such a condition.

Pipra is unlike all of the above. M. tracheolateralis inserts ventrally and ventrilaterally on the anterior edge of the drum; i.e. on A-6 in *P. mentalis* and A-7 in *P. erythrocephala*. M. sternotrachealis inserts on the membranous sheath surrounding M. tracheolateralis. The intrinsic muscle originates broadly near the anterior edge of the drum, immediately posterior to the insertion of M. tracheolateralis. It extends posteriad to insert directly on nearly the entire surface of A-1. In *P. pipra* Müller found no intrinsic muscle. Instead, he described M. tracheolateralis as divided into two fasciculi, which inserted on separate areas of A-1.

Chiroxiphia (Pls. 15 and 16) is unlike all of the above. The Mm. tracheolaterales cover the ventral half of the trachea for most of their length, inserting on the anterior edge of the drum, A-11 in *C. lanceolata* and A-14 in *C. caudata*. M. sternotrachealis is wholly continuous with the superficial lateral fibers of M. tracheolateralis. A broad, thick intrinsic muscle originates on the anterior edge of the drum from the ventral midline to the dorsolateral surface. Müller stated that the muscle consisted of three longitudinal portions, but no such divisions exist in my specimens. The majority of the muscle's mass is in the dorsolateral region. The insertion has three components. In *C. lanceolata* the muscle inserts ventrally by a broad tendon to A-2 and dorsolaterally by two narrow tendons, to the dorsal ends of A-1 and B-1, respectively. *C. caudata* differs only in that the broad ventral tendon is attached to A-1.

Ilicura is unlike all of the above. The Mm. tracheolaterales converge at about A-25 and cover the ventral two-thirds of the trachea to their insertion on A-4 and A-5 ventrally, on A-6 ventrilaterally and, with a dorsolateral extension, on the dorsal end of B-1. The torsion of this muscle is such that fibers from the left muscle insert about 30° to the right of the ventral midline. The Mm. sternotracheales insert on the membranous sheath surrounding the Mm. tracheolaterales, with a few fibers attached directly to A-15 and A-16 at the dorsal edge of the latter muscle.

There is a single pair of intrinsic muscles, which I tentatively call Mm. obliqui ventrales, due to their similarity to those muscles in the Tyrannidae. Each of the pair originates adjacent to the ventral midline of A-2 and A-3 and also ventrally and ventrilaterally on A-4 and A-5. It extends posterolaterally and posterodorsally to insert along nearly the entire length of B-1. At its dorsal edge this muscle is in contact with the extension of M. tracheolateralis.

Corapipo (Pls. 15 and 16) is unlike all of the above. The Mm. tracheolaterales cover the ventral half of the trachea from about A-38 to A-8, where they diverge ventrally and bend dorsad, inserting along a line from the ventrilateral surface of A-7 to the lateral surface of A-4. Approximately the dorsal sixth of the fibers extend to A-1. M. sternotrachealis is extremely robust and inserts directly on the lateral surface of A-15 through A-26, adjacent to the dorsal edge of M. tracheolateralis.

There are two pairs of intrinsic muscles. The ventral one originates immediately posterior to the insertion of M. tracheolateralis, from A-7 to A-4 and on the lateral surfaces of A-3 and A-2. It extends posteroventrad to insert on the ventral end of A-1, wrapping itself around the end of the element. The dorsal muscle originates on the

lateral surface of A-2 and A-3 and extends posterodorsad to insert on the dorsal end of A-1, just lateral to the insertion of the extension of M. tracheolateralis.

FAMILY TYRANNIDAE. TYRANT FLYCATCHERS.

SUBFAMILY FLUVICOLINAE.

Specimens Examined.

Of the 70 species in 27 genera, I have examined the following 46 individuals in 28 species and 21 genera:

Agriornis livida (Kittlitz)
Agriornis microptera Gould
Xolmis coronata (Vieillot)
Xolmis irupero (Vieillot)
Xolmis pyrope (Kittlitz), two specimens
Muscisaxicola albilora Lafresnaye
Muscisaxicola maculirostris Lafr. and D'Orb.
Lessonia rufa (Gmelin)
Neoxolmis rufiventris (Vieillot), two specimens
Ochthoeca fumicolor Sclater, two specimens
Sayornis phoebe (Latham), three specimens
Sayornis nigricans (Swainson)
Sayornis saya (Bonaparte)
Colonia colonus (Vieillot), three specimens
Gubernetes yetapa (Vieillot), two specimens
Yetapa risora (Vieillot)
Knipolegus nigerrimus (Vieillot)
Knipolegus cyanirostris (Vieillot), three specimens
Phaeotriccus hudsoni (Sclater)
Entotriccus striaticeps (Lafr. and D'Orb.)
Lichenops [= *Hymenops*] *perspicillata* (Gmelin)
Muscipipra vetula (Lichtenstein)
Fluvicola climazura (Vieillot)
Arundinicola leucocephala (Linnaeus)
Pyrocephalus rubinus (Boddaert), five specimens
Muscigralla brevicauda (Lafr. and D'Orb.) two specimens
Satrapa icterophrys (Vieillot), two specimens
Machetornis rixosa (Vieillot), three specimens

I know of only the following descriptions by previous authors:

Lessonia rufa (Gmelin) — Müller (1847, p. 35; Pl. 6, fig. 7; 1878, p. 29)
Sayornis phoebe (Latham) — MacGillivray (1839)
Sayornis phoebe (Latham) — Miskimen (1963)
Fluvicola pica (Boddaert) — Müller (1847, p. 35; Pl. 6, figs. 8, 9; 1878, p. 29)
Pyrocephalus rubinus (Boddaert) — Müller (1847, p. 34; Pl. 5, figs. 6. 7; 1878, p. 28)
Machetornis rixosa (Vieillot) — Müller (1847, p. 34; 1878, p. 28)

Cartilaginous Elements.

In *Xolmis* (Pls. 5 and 6), A-1 through A-4 are divided; A-5 and other A-elements are complete. A-2, A-3 and A-4 are weakly fused at their dorsal ends to a triangular plug of soft cartilage which fills the dorsomedial region adjacent to these elements and extends ventrad to connect the ventral ends of the same elements. All of the B-elements are divided. The internal cartilages are rounded triangles, with their pointed ends posteriad and their anterior edges weakly fused to the cartilaginous plug. There is no pessulus, but in the following genera compared with *Xolmis* the pessulus is present unless otherwise noted.

Phaeotriccus is like *Xolmis,* differing as follows. A-3 is double, with the medial section white, spongy cartilage. A-4 is complete and indented mid-dorsally. The pessulus is fused to A-4 at both ends and is completely hidden by the cartilaginous plug.

Pyrocephalus is like *Xolmis,* differing only in that the fusion of the internal cartilages to the plug is more complete. Müller (1847, p. 35) reported the "first bronchial ring," apparently A-2, to be double ("vollstandig") and A-3 complete. In one of my specimens (YPM 2766) A-4 is slightly longer medially than in the other specimens, approaching the double condition. Considering the relative uniformity among my five specimens, Müller's must be considered an extreme variant.

Knipolegus is like *Xolmis,* differing only in that the internal cartilages are completely fused to the cartilaginous plug, with no joint visible.

Neoxolmis is like *Xolmis,* differing as follows. A-5 is divided. In YPM 2736, A-5R is fused dorsally to A-6. The internal cartilages are broader than those of *Xolmis* and slightly crescent-shaped.

Gubernetes is like *Xolmis,* differing as follows. Only A-1, A-2 and A-3 are divided; A-4 is complete and is fused to the cartilaginous plug at the dorsal midline. The internal cartilages are J-shaped, with the curve directed posteriad and ventrad.

Agriornis is like *Xolmis,* differing as follows. In the specimen of *A. livida* there is a supernumerary component, A-4aR, the dorsal end of which does not reach the cartilaginous plug. At its ventral end A-4aR tapers to about one half its usual width and lies very close to A-5. There are two pairs of internal cartilages: one pair completely fused to the cartilaginous plug, consisting of straight bars, and a second pair, posterior to the ends of the first, consisting of short bars oriented at right angles to the first pair.

Fluvicola is like *Xolmis,* but my specimen is too damaged by shot to make detailed analysis possible. All of the A-elements appear to be like those of *Xolmis.*

Muscisaxicola is like *Xolmis,* differing only in that A-5 is divided and fused to the cartilaginous plug, as are A-2 through A-4.

Satrapa and *Entotriccus* are like *Xolmis,* differing as follows. A-4 is not fused to the cartilaginous plug. The proportions of all of the elements are much more delicate than those of *Xolmis;* the membranous interspaces are proportionately wider. The internal cartilages are J-shaped and fused to the cartilaginous plug anteriorly.

Muscipipra appears to be like *Xolmis,* but in my specimen the entire ventral portion of the syrinx was removed by shot, as well as most of the right bronchus and part of the mid-dorsal region. From the remainder the following points can be made out. A-1 through A-3 are divided; A-4 is complete and is fused to the cartilaginous plug. A-2 is not fused to the plug.

Yetapa is like *Xolmis,* differing as follows. A-1 through A-4 are fused dorsally to the cartilaginous plug. These four elements are joined at their ventral ends by a band of soft cartilages. B-1 is strongly curved inward at both ends.

Lichenops (Pls. 7 and 8) is strikingly different from *Xolmis*. A-1, A-2 and A-3 are divided; A-4 and A-5 are incomplete dorsally and are joined at their dorsal ends. All except A-1 are fused dorsally to the cartilaginous plug. The latter has prominent ridges in line with the attached elements. The ventral ends of A-1, A-2, and A-3 are joined by an inverted "U" of soft cartilage, which has an anterior extension lying superficial to the midventral regions of A-4 through A-7 and joined to them. Lying in the midsagittal plane and fused to this "U" is a hook of stiff cartilage directed anteriad.

Colonia (Pls. 5 and 6) is also different from all of the above. A-1, A-2 and A-3 are divided and the remaining A-elements are complete. The concavity of A-1 and A-2 is directed nearly posteriad and at the lateral edge of A-1 is a projecting shelf occupying the middle quarter of the element. In the YPM specimen and the second AMNH specimen A-2 is fused to A-3 at the dorsal end. In the first AMNH specimen the dorsal cartilages are asymmetrical; A-2L and A-3L are fused but A-2R is discrete, while A-3R is fused to A-4. The cartilaginous plug is small and is attached to the dorsal ends of A-2 and A-3 only. It has a medial extension reaching ventrad about two-thirds of the distance to the ventral ends of A-2. The internal cartilages are rounded triangles, flexibly joined to the cartilaginous plug.

Ochthoeca is like the YPM specimen of *Colonia,* differing only in that A-1 lacks the projecting shell.

Muscigralla is like *Colonia,* differing as follows. A-1 and A-2 are divided; A-3 is complete. There is no fusion of elements. The small cartilaginous plug is fused to the dorsal ends of A-2 and to the mid-dorsal posterior edge of A-3. The internal cartilages are long narrow bars fused to the plug and extending posteriad to the level of B-2.

Arundinicola is like *Colonia,* differing as follows. A-3L is fused to a short mid-dorsal posteriad extension of A-4, while A-3R is free. A narrow extra component, A-3aR, located very close to A-4, is also fused dorsally to the same extension. There is a short free pessulus. There are two pairs of internal cartilages: a long dorsal pair lightly attached to the pessulus and extending posteriad to the level of B-2; and a small circular ventral pair fused to the ventral end of the pessulus.

Sayornis also differs markedly from all of the above. None of my specimens shows any fusion of elements. In *S. nigricans* A-1, A-2 and A-3 are divided. A-4 is complete and has a mid-dorsal posteriad extension which curves ventrad, forming the pessulus, free at the ventral end. The pessulus is partially covered by a small cartilaginous plug, attached to the dorsal ends of A-2 and A-3. The internal cartilages are rounded equilateral triangles fused flexibly to the plug. In *S. phoebe* A-1 through A-4 are divided and the pessulus is an extension of A-5. The cartilaginous plug is a transverse bar connecting the dorsal ends of A-2, A-3 and A-4. The internal cartilages are short straight bars fused to the cartilaginous plug and extending posteriad to the level of A-1. *S. saya* differs from *S. phoebe* only in that A-5 and A-6 are incomplete dorsally.

In MacGillivray's description of the syrinx in *S. phoebe* A-1 and A-2 are divided ("dimidiate") and A-3 complete. Miskimen's specimens of *S. phoebe* fit the above description except that A-4, A-5 and A-6 are fused ventrally.

Lessonia (Pls. 5 and 6) is unlike all of the above. A-1 through A-4 are divided; A-5 and A-6 are incomplete dorsally. A-7 is complete and has a long mid-dorsal extension lying between the dorsal ends of A-6, A-5, and A-4. The edges of the

extension are indented to accept the ends of the elements, which are not fused to it. There is no cartilaginous plug and no pessulus. The internal cartilages are shield-shaped, with their broad ends anteriorly, and close to but not fused to the dorsal ends of A-2.

Machetornis (Pls. 7 and 8) is strongly different from all of the above. A-1 is divided and A-2 double; A-3 and other A-elements are complete. A-3 has a mid-dorsal posteriad extension which tapers into an extremely thin pessulus, free at its ventral end. There is no cartilaginous plug. The internal cartilages are small and elliptical and are not fused to any other elements. B-1 consists of a pair of nearly straight bars lying very close to A-1. B-2, whose ends touch those of B-1, consists of a pair of near-semicircles, half as thick as B-1. The bronchi of *Machetornis* are considerably longer and less tapering than those of the above genera.

Musculature.

In *Xolmis pyrope* and *X. irupero,* M. tracheolateralis covers the ventral half of the trachea posterior to A-30. It inserts directly on A-5, ventrally and laterally, mostly near the anterior edge of the element. M. sternotrachealis originates on the interior surface of the coracoid process of the sternum. Near its insertion on the trachea it fans out into a broad flat sheet which inserts on the tough membrane overlying M. tracheolateralis. A few of the dorsal fibers insert directly on the lateral surfaces of A-15 through A-19. M. obliquus ventralis originates along the ventral midline on A-3, A-4 and A-5 as well as ventrilaterally on A-5. The dorsal limit of its origin is in line with the dorsal edge of M. tracheolateralis. The insertion of M. obliquus ventralis covers the center third of A-1. *X. coronata* is identical to the other two, except that the lateral origin of M. obliquus ventralis is on A-4, resulting in a shorter lateral portion of the muscle.

Neoxolmis is like *Xolmis,* differing as follows. M. tracheolateralis inserts along a line extending from A-4 ventrally to A-2 laterally. M. obliquus ventralis originates midventrally on A-2, A-3, and A-4 and posterior to the insertion of M. tracheolateralis. Its insertion is along the ventral two-thirds of A-1, except for a small part of the ventral end. The two specimens differ in the region of insertion of M. sternotrachealis, but in both the mode of insertion is as in *Xolmis.* In YPM 2739 the insertion is at the level of A-13 through A-23; in YPM 2736 it is at A-26 through A-33.

Entotriccus is like *Xolmis,* differing as follows. The dorsal third of M. sternotrachealis, instead of inserting directly, is continuous with the superficial fibers of M. tracheolateralis. The superficial fibers of M. obliquus ventralis originate midventrally on A-3, A-4 and A-5 and only slightly off the ventral midline on A-5. The deeper fibers attach to A-4 from the ventral midline about halfway to the dorsal midline. A few of the fibers at the dorsal edge of the muscle originate on A-3. The insertion is on the center third of A-1, as in *Xolmis.*

Gubernetes is like *Xolmis,* differing as follows. M. tracheolateralis inserts along the anterior edge of the ventral two-thirds of A-3. M. sternotrachealis has two fasciculi, a ventral one which inserts on the membrane covering M. tracheolateralis, and a dorsal one, about one-third of the muscle, inserting on A-10, A-11, and A-12 adjacent to the dorsal edge of M. tracheolateralis. M. obliquus ventralis originates on the edge of A-3, posterior to the insertion of M. tracheolateralis, and inserts on the center third of A-1.

Muscipipra appears to be like *Xolmis,* but shot damage prevents positive comparisons of the ventral muscles. M. tracheolateralis covers the ventral half of the trachea from A-28 to its insertion on A-3 laterally and probably on A-4 ventrally. M. sternotrachealis has two fasciculi: the dorsal one inserting directly on A-14 through A-19 and the ventral one continuous with M. tracheolateralis. The lateral fibers of M. obliquus ventralis originate on A-3 and insert on A-1.

Fluvicola is like *Xolmis,* differing as follows. M. tracheolateralis inserts on A-4 ventrally and on A-3 laterally. M. sternotrachealis is proportionately heavier than in *Xolmis* and has only slight continuity with M. tracheolateralis, the majority of the fibers inserting on the membranous sheath surrounding the latter muscle. The ventral fibers insert on a median raphe which is continuous with the sheath. M. obliquus ventralis originates on A-3 and A-4 ventrally and on A-3 laterally, inserting as in *Xolmis.*

Satrapa is like *Xolmis,* differing as follows. In addition to its ventral insertion on A-5, M. tracheolateralis sends a lateral extension to insert on A-2 beneath M. obliquus ventralis. M. sternotrachealis is very thin and inserts directly on A-16 through A-21, adjacent to the dorsal edge of M. tracheolateralis.

Agriornis is like *Xolmis,* differing as follows. M. tracheolateralis inserts on A-5 and is very thick ventrally. M. sternotrachealis is thin (about one-sixth the diameter of the trachea) and inserts adjacent to the dorsal edge of M. tracheolateralis on A-12 through A-14 in *A. livida* and on A-10 through A-13 in *A. microptera.* In both specimens M. obliquus ventralis originates on A-5 ventrally and A-4 laterally as well as on the A-4/A-5 membrane. It inserts on A-1. The muscle has distinct ventral and lateral parts, but both the origin and insertion are continuous from one edge of the muscle to the other.

Lessonia (Pls. 5 and 6) is unlike all of the above. M. tracheolateralis covers the ventral half of the trachea posterior to A-38, inserting on A-3 ventrally and on A-4 laterally. M. sternotrachealis is very thick (about half the diameter of the trachea). Its insertion is slightly asymmetrical: the posterior edge of the right muscle is at A-5, that of the left at A-6. The posterior half of each muscle inserts on the membranous sheath surrounding the Mm. tracheolaterales. The two Mm. sternotracheales interdigitate ventrally from A-6 to about A-12. The anterior fibers are continuous with the lateral superficial ones of Mm. tracheolaterales. M. obliquus ventralis is small, originating on A-3 and extending parallel to the bronchial axis to its insertion on the ventral quarter of A-1. Müller's description of *Lessonia* stated only that the tracheal and syringeal muscles are like those of *Fluvicola bicolor.*

Phaeotriccus is like *Lessonia,* differing as follows. About one-tenth of the fibers of M. sternotrachealis, at the posterior edge of the muscle, are continuous from one member of the pair to the other. M. obliquus ventralis originates on a median raphe attached midventrally to A-2 and A-3.

Muscisaxicola is like *Lessonia,* differing as follows. The Mm. sternotracheales are symmetrical and their insertion on the sheath extends from A-8 to A-15, beyond which the fibers are continuous with the Mm. tracheolaterales. A narrow extension of M. tracheolateralis near the dorsal edge reaches A-1 adjacent to M. obliquus ventralis. The latter originates directly on A-3 midventrally and on A-4 ventrally and laterally; the insertion is on A-1.

Knipolegus is like *Lessonia,* differing as follows. M. sternotrachealis inserts more

anteriorly, at the level of A-12 through A-18. The posterior tenth of the fibers are continuous from one of the pair to the other. A few of the dorsal fibers insert directly on A-11 through A-14 at the dorsal edge of M. tracheolateralis. The M. obliquus ventralis originates near the ventral midline on A-2 through A-5, directly. It extends posterolaterally to insert broadly in the center of A-1.

Lichenops (Pls. 7 and 8) differs markedly from all of the above. M. tracheolateralis covers the ventral half of the trachea from A-46 to its insertion on A-6. M. sternotrachealis is very thick, its longer diameter being about one-third that of the trachea. Its insertion is almost entirely on the membranous sheath around M. tracheolateralis, a few of the dorsal fibers inserting directly on the lateral surfaces of A-13 through A-16. The origin of M. obliquus ventralis covers a large area, ventrally on the cartilaginous hook and on the tough vane enclosed by it; laterally and dorsolaterally on A-5 and A-6. The direction of the superficial fibers is nearly anteroposterior; the deep fibers run almost at right angles to them, the transition being gradual. The insertion covers nearly the entire length of A-1 and a small portion of the ventral end of the A-1/B-1 membrane. The belly of the muscle bulges so strongly that it covers the insertion of M. tracheolateralis.

Sayornis (Pls. 5 and 6) also differs widely from all of the above. In all three species, M. tracheolateralis covers the ventral half of the trachea from the convergence of the pair in the low A-30's (variable) to its insertion ventrally on A-2 and laterally on the anterior edge of A-1. In *S. phoebe* and *S. saya* the insertion of M. sternotrachealis is directly on approximately A-10 through A-13 (variable) at the dorsal edge of M. tracheolateralis. In *S. nigricans,* M. sternotrachealis reaches M. tracheolateralis at the level of A-10 and A-11, passes through the latter muscle in small fasciculi and inserts directly on A-10 and A-11 beneath M. tracheolateralis. In *S. nigricans* and *S. phoebe,* M. obliquus ventralis has two layers. The superficial one is a continuous band of fibers extending from the ventral half of A-1L to the corresponding portion of A-1R. In a sense, this band, being symmetrical, has two insertions and no origin. The deep layer originates near the ventral midline on A-2 through A-5, both directly and by a short raphe. It extends posterolaterally to insert on A-1 just anterior to the insertion of the superficial layer. *S. saya* lacks the superficial layer but is otherwise similar to the other members of the genus.

Miskimen (1963) gave quite a different description of the syrinx of *S. phoebe.* In her two specimens she found M. tracheolateralis inserting on A-8. M. obliquus ventralis apparently originated in the same manner and location as the deeper layer of my specimens, but the superficial layer was lacking, as in *S. saya.* Moreover, she found the muscle inserting on the dorsal ends of A-1, A-2 and A-3.

Arundinicola is like *Sayornis,* differing as follows. M. tracheolateralis inserts ventrally on A-4, ventrilaterally on A-5, and laterally on A-4. M. sternotrachealis inserts directly at the dorsal edge of M. tracheolateralis on the lateral surface of A-10 through A-13. M. obliquus ventralis originates midventrally on A-2 and A-3 and inserts in the center of the A-1/B-1 membrane. The anterior third of the fibers are continuous from one side to the other, superficial to the insertion of M. tracheolateralis.

Muscigralla is like *Sayornis,* differing as follows. M. tracheolateralis inserts ventrilaterally and laterally on A-2. M. sternotrachealis inserts partly on the ventral part of the sheath around M. tracheolateralis and partly as in *Sayornis,* on A-11, A-12 and

A-13. M. obliquus ventralis originates on a median raphe attached to the ventral ends of A-2 through A-4, and extends, superficial to the insertion of M. tracheolateralis, to insert on the ventral half of A-1.

Pyrocephalus (Pls. 7 and 8) is very different from all of the above genera. M. tracheolateralis covers the ventral half of the syrinx posterior to about A-28 (variable). The lateral fibers insert on A-4, while the main part of the muscle tapers almost to a point midventrally, inserting on A-2 and A-3 near the ventral midline. M. obliquus ventralis originates on the ventral region of A-2 and A-3 adjacent to the point of M. tracheolateralis and inserts near the center of the A-1/B-1 membrane. Although a narrow muscle, compared with that of many tyrannids, it is variable. In YPM 2177 M. obliquus ventralis is only about one-third the width of M. tracheolateralis; in YPM 2768 the former is nearly as wide as the latter; the other three specimens are intermediate. Müller's description and illustration of the syrinx of *Pyrocephalus* closely approximates that of my specimen YPM 2177.

Yetapa is like *Pyrocephalus,* but the specimen at hand appears to have been dried in preparation, making accurate comparison difficult. The following differences are apparent. M. sternotrachealis inserts wholly on the lateral surfaces of A-19 through A-26. M. obliquus ventralis originates along the ventral half of A-3 and inserts on the A-1/B-1 membrane. It is broader than in any of the specimens of *Pyrocephalus,* being the full width of M. tracheolateralis.

Colonia (Pls. 5 and 6) differs markedly from all of the above. M. tracheolateralis covers the ventral two-thirds of the trachea from about A-31 to its insertion on A-3 ventrally and A-4 laterally. M. sternotrachealis is wholly continuous with the superficial fibers of M. tracheolateralis, which it meets at the level of A-16. M. obliquus ventralis originates on A-2 near the ventral midline, on the connective tissue between A-2 and A-3, and laterally along A-3 about two-thirds of the distance to the dorsal midline. In the first and third specimens listed the fibers are strongly bunched at the dorsal and ventral edges of the muscle, leaving it thin in the middle. In the second specimen, the muscle is of uniform thickness. In all three the origin is continuous over its entire width. The insertion is on the projecting shelf in the center of A-1.

Ochthoeca is unlike all of the above. M. tracheolateralis consists of a narrow lateral strip, broadening near its insertion, on the lateral two-thirds of A-4 and dorsolaterally on A-5. The members of the pair meet ventrally at A-6. M. sternotrachealis inserts directly on A-14 through A-18, at the dorsal edge of M. tracheolateralis. M. obliquus ventralis originates on the ventral half of A-4 with some of the deep fibers attached to A-3. It inserts along the ventral half of A-1, except for the extreme ventral end. M. obliquus dorsalis (see Pl. 1, fig. 6,) originates by a short raphe on the dorsal midline of A-4 and A-5. It extends posterolaterally to insert directly on a small area of A-1 adjacent to the insertion of M. obliquus ventralis.

Machetornis (Pls. 7 and 8) is unlike all of the above. M. tracheolateralis covers the ventral half of the trachea from A-40 (variable) to A-5 (all specimens) where the members of the pair diverge. It inserts directly on the ventral half of A-1. M. sternotrachealis inserts ventrally on the membranous sheath around M. tracheolateralis, laterally in continuity with the superficial fibers of the latter, and dorsally on A-12 through A-17. The direction of M. sternotrachealis is such that it lies against M. tracheolateralis at the level of A-3. There are no intrinsic muscles.

SUBFAMILY TYRANNINAE.

Specimens Examined.

Of 34 species in 13 genera, I have examined the following 29 individuals in 19 species and 12 genera:

Muscivora tyrannus (Linnaeus)
Tyrannus tyrannus (Linnaeus), three specimens
Tyrannus albogularis Burmeister
Tyrannus melancholicus Vieillot
Tyrannus dominicensis (Gmelin)
Empidonomus aurantioatrocristatus (Lafr. and D'Orb.)
Legatus leucophaius (Vieillot)
Sirystes sibilator (Vieillot), two specimens
Myiodynastes luteiventris Sclater, three specimens
Myiodynastes bairdii Gambel
Megarhynchus pitangua (Linnaeus)
Conopias trivirgata (Wied)
Myiozetetes cayanensis (Linnaeus), three specimens
Myiozetetes similis (Spix), three specimens
Myiozetetes granadensis Lawrence
Tyrannopsis sulphurea (Spix)
Pitangus sulphuratus (Linnaeus), two specimens
Pitangus lictor Lichtenstein
Tolmarchus caudifasciatus (D'Orbigny)

I know of only the following descriptions in literature:

Muscivora tyrannus (Linnaeus) — Miskimen (1963)
Tyrannus melancholicus Vieillot — Müller (1847, p. 34; 1878, p. 28)
Tyrannus tyrannus (Linnaeus) — MacGillivray (1839, p. 421)
Tyrannus tyrannus (Linnaeus) — Miskimen (1963)
Pitangus sulphuratus (Linnaeus) — Müller (1847, p. 33; Pl. 3, figs. 1-5; 1878, p. 27)

Cartilaginous Elements.

Tyrannus (Pls. 9 and 10) is typical of a large section of the subfamily. In *T. tyrannus* A-1 is divided. A-2 is double; the medial portion of each component is very straight and meets the lateral portion with a noticeable "corner." The two components are fused at their ventral ends. A-3 and A-4 are variable among my specimens. In YPM 706 A-3 is divided, A-4 incomplete dorsally, and A-5 complete. In YPM J-761 A-4 is complete and in the unnumbered specimen both A-3 and A-4 are complete. In YPM 706 and YPM J-761 the pessulus is a small rigid bar extending from the space between the dorsal ends of A-3, about two-thirds of the distance to the ventral junction of A-2. The pessulus is lacking in the unnumbered specimen. The B-elements are narrow (about half as wide as the A-elements), divided, and lie parallel to A-1. B-1 and B-2 are connected by a short bridge of cartilage at their ventral ends. Each B-element posterior to B-4 has a bony cap covering the middle third of the component.

The internal cartilages are straight bars flexibly attached to the dorsal ends of A-2 and extending posteriad to the level of B-2. YPM 706 will serve as the basis for comparison with other genera.

Tyrannus melancholicus and *T. dominicensis* are like *T. tyrannus* in all respects. *T. albogularis* differs only in that A-4 is divided and A-5 is incomplete ventrally.

Müller stated that in *Tyrannus melancholicus* A-2, A-3, and A-4 are double ("ganze") but gave no other information. In *T. tyrannus*, MacGillivray found A-1 and A-2 divided and the pessulus lacking. Miskimen's description of *T. tyrannus* agrees with that of YPM 706 (above), except that in her specimen A-4 is divided instead of incomplete dorsally. Instead of fusion, elements A-1 through A-4 are joined by connective tissue. The pessulus is lacking.

Muscivora is like *Tyrannus*, differing as follows. A-3, A-4, and A-5 are incomplete ventrally. A-1 through A-4 are fused at their ventral ends and for about one-third of their lengths. There is no pessulus. The internal cartilages are J-shaped with the curved section directed ventrad. They are fused to the dorsal "corners" of A-2.

Miskimen's description of *Muscivora* agrees with the above, except that in her specimen both A-3 and A-4 ("syringeo-bronchial rings") were double and only A-3, A-4, and A-5 ("drum") were fused ventrally. A-5 was complete, and the pessulus was lacking.

Tyrannopsis is like *Tyrannus*, differing only in that the lower A-elements are proportionately narrower and the internal cartilages slightly longer.

Myiodynastes is like *Tyrannus*, differing as follows. The two components of A-2 do not touch. Both A-3 and A-4 are divided. A-5 has a short midventral extension filling the space between the ventral ends of A-4. On YPM 1047 this extension is lacking and in its place is a small bony disc attached to the ventral end of the pessulus. The latter is a cartilaginous bar constituting the ventral half of the junction of the internal tympaniform membranes.

Megarhynchus is like *Tyrannus*, differing as follows. The ventral ends of A-1 and A-2 do not touch their opposite members. The region between the ventral ends of A-3 is membranous, but the internal tympaniform membranes extend to the level of A-4, so that the ventral ends of A-3 have the air sac on both sides of them. The mid-dorsal region differs from that of *Tyrannus* in having a broad plug of cartilage extending from the medial sections of A-2 to the middle of A-4, replacing the pessulus. The ventral ends of B-3 are held in contact by tough connective tissue. The internal cartilages are J-shaped, with the short arm directed ventrad.

Tolmarchus is like *Tyrannus*, differing as follows. The dorsomedial corner of A-2 is rounded. The pessulus is a small plate located between the medial sections of A-2 and fused to them ventrally.

Conopias is like *Tyrannus*, differing as follows. A-4 is complete, as are the anterior A-elements. In the region of B-3 through B-6 the bronchi are so close that the ventral ends of the elements dovetail and are held in that position by tough connective tissue. The internal cartilages are J-shaped.

Empidonomus is like *Tyrannus*, differing as follows. A-1, A-2, and A-3 are about half the width of the other elements and are unfused. A-4 and A-5 are completely fused. The internal cartilages are short, extending only to the level of B-1. There is no pessulus.

Pitangus sulphuratus and *P. lictor* differ considerably from each other. *P. sulphur-*

atus is like *Tyrannus*, differing as follows. A-2 through A-5 are double and are closely fitted together, but not fused. There is no pessulus; its place is occupied by the medial portions of A-4 and A-5. The B-elements are unusually stiff but are divided and shaped as in other genera. B-1 is in contact with A-1 for most of its length. B-2 touches B-1 only at its ends, which are thickened and spatulate. B-3 and B-4 are connected ventrally by a stiff bar forming a "U" and the two "U's" are held together by fibrous connective tissue. Müller's description of *Pitangus* is like the above, except that he neither mentioned nor illustrated the bar connecting B-3 and B-4.

Pitangus lictor is markedly different from *Tyrannus*. A-2 is divided, but nearly double, the medial section extending about three-quarters of the distance from the dorsal to the ventral side. The medial portion is broader than the lateral portion of the element and is made of spongy white cartilage. A-3 is like A-2 except that the medial section is narrow, stiff and transparent. A-4 and A-5 are divided rings of the usual C-shape. A-6 and remaining A-elements are complete. The internal cartilages are short narrow bars attached to the dorsal end of the medial section of A-2. There is no pessulus.

Legatus (Pls. 7 and 8) differs strongly from all of the above. A-1, A-2, and A-3 are divided; A-4 is incomplete ventrally. A-2 and A-3 are fused for their dorsal halves only. A cartilaginous plug fills the mid-dorsal region from A-4 (to which it is fused) about two-thirds of the way to the ventral side of the internal tympaniform membranes. It is fused to the dorsal ends of A-2 and A-3. The pessulus is a median bony plate completely covered by the plug and extending from the region between the dorsal ends of A-3 halfway to the ventral ends of that element. The internal cartilages are J-shaped and are not attached to other elements.

Sirystes differs from all of the above. In YPM 2790, A-1 through A-4 are divided and A-5 and subsequent elements are complete. A-4L is completely fused to A-5. The cartilaginous plug is saddle-shaped, extending dorsally to the ends of A-2, A-3, and A-4 (to which it is fused) and ventrally to about midway between the dorsal and ventral surfaces. There is no pessulus. The internal cartilages are J-shaped, with the curved part directed ventrad. All the B-elements are divided, with slightly spatulate ends. The other specimen, YPM 2791, differs from the first in that A-4 is incomplete ventrally and wholly free from A-5. All of the elements are narrower than those of YPM 2790, with wider membranes between them. The cartilaginous plug is attached to A-2 and A-3 only. The internal cartilages are J-shaped with the short arm directed ventrad.

Myiozetetes is unlike all of the above, and the seven specimens vary among themselves. Because of its symmetry YPM 1543 (*M. similis*) will be described as "typical" (Pls. 9 and 10). A-1 is divided; A-2 is double, the two medial sections being fused at their ventral ends; A-3, A-4, and A-5 are divided; A-6 and A-7 are complete and are fused over their entire length; A-8 is complete and unmodified. The pessulus is a stiff, narrow plate extending from the region between the dorsal ends of A-5 to the ventral ends of A-2, which it touches. The internal cartilages are straight, are attached to the dorsomedial region of A-2, and extend to the level of B-1. In YPM 2174 both A-2 and A-3 are double and fused along their dorsal halves, with A-2 contributing most of the medial section; A-4 is divided; A-5, A-6, and A-7 are complete and fused; A-8 and subsequent elements are complete and unmodified. The pessulus is short, extending from between the dorsal ends of A-4 about halfway to

the ventral ends of A-3. YPM 1021 differs from YPM 2174 in that A-5, A-6, and A-7 are free. The pessulus is fused to A-5 dorsally and extends to the ventral ends of A-3.

Myiozetetes cayanensis is like *M. similis* (YPM 1543) except as follows. YPM 2024 lacks all fusion. In YPM 1769 A-5 is complete and there is no fusion. The pessulus is fused to the dorsal end of A-4L. In YPM 1844 A-5, A-6, and A-7 are fused and only A-3L is fused to A-2. The pessulus, fused dorsally to A-5, extends only about halfway to the ventral end of A-3. *M. granadensis* is like the "typical" *similis* except that A-4 and A-5 are complete and fused. There is no other fusion and no pessulus.

Musculature.

In *Tyrannus tyrannus* (Pls. 9 and 10), *T. melancholicus,* and *T. dominicensis* the Mm. tracheolaterales converge ventrally at about A-27 (variable) covering the ventral half of the trachea to about A-9, where they diverge slightly. Their insertion lies along a pair of spiral lines from A-4 ventrally to A-6 dorsolaterally. M. sternotrachealis originates on the interior surface of the coracoid process of the sternum. Near its insertion it divides into three fasciculi which insert, respectively, on the ventral portion of the membranous sheath surrounding M. tracheolateralis, in continuity with the lateral fibers of the latter, and dorsolaterally directly on A-10 through A-16, adjacent to the dorsal edge of M. tracheolateralis.

M. obliquus ventralis protrudes strongly on each side of the syrinx. It originates directly on A-3 and A-4 ventrilaterally and on A-4 and A-5 laterally and dorsolaterally, the deeper fibers being attached to the more posterior element. The muscle extends posterodorsad to insert directly on the dorsal tenth of A-1, on the dorsal fifth of B-1, and by a narrow tendon to the center of the B-1/B-2 membrane. The deep fibers are oriented anteroposteriorly, the superficial ones more dorsoventrally.

Tyrannus albogularis is like *T. tyrannus* except that the muscles are less strongly developed.

Müller's brief description of *T. melancholicus* agrees closely with the above. Miskimen's description of *T. tyrannus*, based on three individuals, is quite different from the above. She found M. tracheolateralis inserting on the dorsal end of A-3 ("bronchial bar 2") and on the ventral part of A-5 ("drum"). In describing M. sternotrachealis she stated that it inserts on M. tracheolateralis and on A-11 ("tracheal ring 6"). M. obliquus ventralis she described as above, but without the tendinous insertion to the B-1/B-2 membrane.

Muscivora is like *Tyrannus,* differing as follows. M. tracheolateralis inserts entirely on A-7. M. sternotrachealis is more robust and some of the ventral fibers are continuous between the right and left muscles. The dorsal fasciculus inserts on A-9 through A-14. The Mm. obliqui ventrales touch at the ventral midline. They originate on A-7 superficially, on A-6, and on A-5 deeply and insert superficially on the dorsal half of B-1 and deeply on the dorsal end of A-1.

Miskimen's specimen of *Muscivora* differed from the above in lacking the direct insertion of M. sternotrachealis and the insertion of M. obliquus ventralis on B-1.

Myiodynastes is like *Tyrannus,* differing as follows. The Mm. tracheolaterales are very narrow, do not converge ventrally, and insert on A-6 only. The Mm. sternotracheales are asymmetrical; the right inserts partly directly on A-12 through A-15, on both sides of the ventral midline, and partly in continuity with M. tracheolateralis; the left is wholly continuous with M. tracheolateralis. The Mm. obliqui ventrales are

widely spaced ventrally, originating mostly on A-6, with a few superficial fibers attached to A-7 dorsolaterally. They insert on the dorsal third of A-1, adjacent parts of the A-1/A-2 membrane, the dorsal tip of B-1, and the intervening part of the A-1/B-1 membrane.

In my specimen of *Tyrannopsis* much of the syringeal musculature was eaten by ants, but it is certain that the positions of the muscles were as in *Tyrannus*. Evidently the Mm. obliqui ventrales were strongly protruding, to judge from the direction of the remaining fibers.

Megarhynchus is like *Tyrannus,* differing as follows. The Mm. tracheolaterales converge midventrally at A-26 and remain in contact to their insertion, on A-4 and A-5. Most of the fibers of M. sternotrachealis are in the ventral fasciculus, which inserts broadly on the membranous sheath of M. tracheolaterales. M. obliquus ventralis is shorter and broader than in *Tyrannus*. It originates in an elliptical area covering A-5 laterally (superficial fibers), most of A-4, and A-3 laterally (deep fibers). It inserts directly on the dorsal ends of A-1 and B-1, on the A-1/B-1 membrane, and also by a broad thin tendon to the B-1/B-2 membrane and the dorsal end of B-2.

The two species of *Pitangus* differ sharply from each other. *P. sulphuratus* is like *Tyrannus,* differing as follows. M. tracheolateralis is narrow and lateral, inserting on A-4 only. M. sternotrachealis inserts directly on A-13 through A-17. M. obliquus ventralis is broader and thicker than in *Tyrannus*. It originates near the ventral midline on A-3 through A-7 and around to the dorsolateral surfaces of A-5, A-6, and A-7. A few short, deep fibers extend from A-3 to A-2; the remainder of the muscle inserts on the dorsal third of A-1 and B-1, the dorsal tip of B-2, and (a few fibers) on the intervening part of the B-1/B-2 membrane. Müller's description of *P. sulphuratus* agrees closely with the above.

In *P. lictor,* M. tracheolateralis is narrow and lateral and inserts on A-6. M. sternotrachealis has two fasciculi, the ventral one of which, less than a quarter of the muscle, is continuous with M. tracheolateralis. The rest of the muscle inserts directly on A-15 and A-16, at the dorsal edge of M. tracheolateralis. M. obliquus ventralis originates along the ventral midline on A-3 through A-7 and around to the dorsolateral part of A-7; it inserts with a broad tendon to the dorsal third of B-1.

Tolmarchus is like *Tyrannus,* differing as follows. M. sternotrachealis has only two fasciculi, a ventral one inserting on the membranous sheath of M. tracheolateralis, and a dorsal one inserting directly on A-9, A-10, and A-11. M. obliquus ventralis originates along a line from the ventrilateral region of A-4 across A-5 to the dorsolateral region of A-6. It inserts directly on the dorsal end of the B-1/B-2 membrane, with no apparent attachment to the elements themselves.

Conopias is like *Tyrannus,* differing as follows. M. tracheolateralis is narrower and thicker, and situated laterally, inserting on A-5. The left M. sternotrachealis has three fasciculi; the right only two. In the latter, one fasciculus is continuous with M. tracheolateralis, while the other inserts directly on A-13, A-14, and A-15. M. obliquus ventralis originates ventrilaterally on A-4 and dorsolaterally on A-5; it inserts on the dorsal end of B-1, with a few fibers attached to the adjacent membranes.

Empidonomus is like *Tyrannus,* differing as follows. The Mm. tracheolaterales nearly surround the trachea, leaving a very narrow space mid-dorsally and a slightly wider one posterior to their divergence ventrally at A-9. M. sternotrachealis inserts dorsally and ventrally on the membranous sheath surrounding M. tracheolateralis

and laterally in continuity with the latter. M. obliquus ventralis originates all along the insertion of M. tracheolateralis. Most of the muscle mass is in the dorsal and dorsolateral regions. It inserts on the dorsal quarter of B-1.

Legatus (Pls. 7 and 8) differs markedly from all of the above. M. tracheolateralis is narrow and lateral, broadening slightly near its insertion, on A-7 and A-6 ventrilaterally and on A-5 dorsolaterally. The thin M. sternotrachealis inserts adjacent to the dorsal edge of M. tracheolateralis, on A-11 through A-18. The left M. obliquus ventralis is longer than the right, originating slightly to the right of the ventral midline on A-7 and on the midline of A-6 and A-5. It extends posterolaterally to insert by a tough, transparent tendon to the dorsal end of B-1. The tendon overlies that of M. obliquus lateralis and the two are lightly attached where they pass over A-1. The right muscle originates just to the right of its sibling and inserts in the same manner. M. obliquus lateralis originates on the lateral surface of A-5 and extends posteriad to insert by a broad tendon to the ventral half of B-1.

Myiozetetes (Pls. 9 and 10) is like *Legatus,* differing as follows. In all specimens the Mm. tracheolaterales are very close ventrally but do not touch. In *M. cayanensis, M. granadensis* and two specimens of *M. similis* (YPM 1543 and 2174) the insertion is on A-6 ventrally and A-7 laterally. In the third specimen of *M. similis* (YPM 1021) it is on A-5 ventrally and A-6 laterally. M. sternotrachealis is thin in all individuals. It inserts directly on two or three elements in the region of A-14, except in YPM 1024 (*M. cayanensis*), in which the ventral third of the fibers are continuous with the dorsal fibers of M. tracheolateralis. The Mm. obliqui ventrales are symmetrical, originating, in all specimens, along the ventral midline from A-3 to a point just posterior to the insertion of the Mm. tracheolaterales. Each of the oblique muscles extends posterodorsally to insert by a narrow tendon to the dorsal end of A-1. In *M. cayanensis* and in one specimen of *M. similis* (YPM 1021) the ventral half of this muscle inserts on the broad tendon of M. obliquus lateralis. The latter originates just posterior to the lateral insertion of M. tracheolateralis, and inserts by a broad tendon to the ventral half of B-1.

Sirystes is unlike all of the above. M. tracheolateralis, thin and narrow, lies on the ventrilateral surface of the trachea and inserts on the anterior edge of A-5. M. sternotrachealis inserts adjacent to the dorsal edge of M. tracheolateralis on A-9, A-10, and A-11. M. obliquus ventralis originates near the ventral midline of A-3, A-4, and A-5 and laterally on A-5. It extends posterodorsally to insert on the center third of A-1. The musculature of YPM 2791 is considerably more slender than that of YPM 2790.

SUBFAMILY MYIARCHINAE.

Specimens Examined.

Of the 78 species in 21 genera (including *Aechmolophus* Zimmer 1938), I have examined the following 34 specimens of 26 species in 16 genera:

Myiarchus crinitus (Linnaeus), three specimens
Myiarchus brachyurus Ridgway
Myiarchus tyrannulus (Müller)
Myiarchus ferox (Gmelin)

Myiarchus tuberculifer (Lafr. and D'Orb.), two specimens
Eribates magnirostris (Gould), two specimens
Nesotriccus ridgwayi Townsend
Nuttallornis mesoleucus (Lichtenstein)
Myiochanes [= *Contopus*] *virens* (Linnaeus), two specimens
Myiochanes cinereus (D'Orbigny)
Blacicus carribaeus (D'Orbigny)
Empidonax flaviventris (Baird)
Empidonax minimus (Baird), three specimens
Empidonax difficilis Baird
Empidonax albigularis Sclater and Salvin
Empidonax oberholseri A. R. Phillips
Aechmolophus mexicanus Zimmer
Cnemotriccus poecilurus (Sclater)
Mitrephanes phaeocercus (Sclater)
Terenotriccus erythrurus (Cabanis)
Aphanotriccus capitalis (Salvin)
Myiobius sulphureipygius (Sclater)
Myiobius atricaudatus Lawrence
Pyrrhomyias cinnamomeus (Lafr. and D'Orb.)
Myiophobus fasciatus (Müller)
Onychorhynchus coronatus (Müller), two specimens

I know of the following descriptions by previous authors:

Myiarchus crinitus (Linnaeus) — MacGillivray (1838, p. 423)
Myiarchus crinitus (Linnaeus) — Miskimen (1963)
Myiarchus stolidus (Gosse) — Maynard (1928, p. 143)
Myiarchus ferox (Gmelin) — Müller (1847, p. 34; 1878, p. 28)
Myiochanes virens (Linnaeus) — MacGillivray (1838, p. 426)
Myiochanes virens (Linnaeus) — Maynard (1928, p. 138)
Myiochanes virens (Linnaeus) — Miskimen (1963)
Empidonax minimus (Baird) — MacGillivray (1838, p. 427)
Empidonax minimus (Baird) — Maynard (1928, p. 135)
Empidonax traillii (Audubon) — Miskimen (1963)
Empidonax virescens (Vieillot) — MacGillivray (1838, p. 427)
Terenotriccus erythrurus (Cabanis) — Müller (1847, p. 35; Pl. 5, fig. 8; 1878, p. 29)

Cartilaginous Elements.

Myiarchus crinitus (Pls. 9 and 10) is typical of the genus. There is considerable variation among my specimens, particularly in the configuration of A-3. In all three A-1 is divided and A-2 is double. In YPM 759 the medial portion of A-2 has a short section of porous white cartilage narrower than the rest of the element. A-3 is divided. A-3R has a medial extension about halfway to the ventral end of the element. This condition is found in both halves of A-3 in the unnumbered specimen, but not at all in YPM 1122. A-4 and other A-elements are complete. In YPM 759 and 1122 A-4 and A-5 are fused, while in the unnumbered specimen it is A-5 and A-6. The B-

elements are uniform among my specimens. All are divided and only the dorsal end of B-1 is spatulate. There are two pairs of internal cartilages. The dorsal pair are thick, large and J-shaped with the short arm directed ventrad and the long arm terminating anteriorly near the dorsomedial edge of A-2. The anterior ends of this pair are connected by a cartilaginous plug in the form of a bar at right angles to the sagittal plane. The ventral pair are short, thick bars lying ventral to the short arm of the dorsal pair, and aligned with it. There is no pessulus. *M. brachyurus* is like *M. crinitus* (unnumbered specimen).

M. tuberculifer is also like *M. crinitus,* except as follows. In YPM 1889 the dorsal end of A-3R is connected to A-4 by a short intermediate section and a similar section joins A-4 and A-5 mid-dorsally. In YPM 1040 these connections are lacking, but A-5 and A-6 are fused for about 30° on each side of the ventral midline. *M. ferox* is like *M. crinitus* (unnumbered) differing only in that A-3 is double, the medial portion being narrow and opaque. In addition the dorsal half of A-4 is fused to A-5 and the whole of A-5 to A-6. *M. tyrannulus* is like *M. crinitus,* except that A-1 through A-4 are divided and A-5 is incomplete ventrally. A-4L is fused to A-5 dorsally and to A-5R ventrally, leaving the ventral end of A-5L free. A-6 and A-7 are fused on the left side.

Müller's description and illustration of *M. ferox* agree closely with the above. In *M. stolidus* Maynard described and figured a "syringeal box" of divided elements, A-1 through A-4, closely fitted but not fused. He did not mention the pessulus or the internal cartilages. In *M. crinitus* Miskimen found the elements to be like those of my YPM 759, but with A-2 divided and a partial fusion of A-4 and A-5.

Eribates is like *Myiarchus* (unnumbered), differing as follows. A-2 is divided. In USNM 20541 A-4 and A-5 are fused for their dorsal halves. The bridge between the internal cartilages is larger and its junction with the cartilages less distinct. In USNM 223306 the bridge has a ventral extension almost reaching the ventral surface at A-2. The smaller pair of internal cartilages is absent.

Myiophobus is like *Myiarchus,* differing as follows. A-4 and A-5 are divided; A-6 is incomplete dorsally. The pessulus extends in an arc from between the ventral ends of A-5 to the region between A-4 and A-5 mid-dorsally, where it is fused to A-4R and A-5L. The internal cartilages are straight flat bars attached to the dorsomedial region of A-2 and extending posteriad to the level of B-1. The connecting bridge and the smaller pair of internal cartilages are absent.

Terenotriccus (Pls. 11 and 12) is unlike all of the above. A-1 is divided; A-2 and A-3 are double; A-4 is divided; A-5 and other A-elements are complete. There is an extra divided component, A-4aR. The pessulus is fused dorsally to A-4L and extends to the ventral ends of A-4, where it is not fused. The internal cartilages are thin and slightly hooked ventrad. Müller's brief mention of this genus stated only that two elements (A-2 and A-3) are double.

Onychorhynchus is like *Terenotriccus,* differing as follows. In both individuals the extra component is "double" and seems best designated A-3aR. A-4 is incomplete dorsally and is joined ventrally to A-3aR by a midventral extension. The internal cartilages are flat plates in the shape of a two-kerneled peanut, oriented with the long axis dorsoventrally. Each is connected to the respective dorsomedial region of A-2 by a thin strand of cartilage from the dorsal end of the "peanut." In the male specimen the medial side of each plate is covered by a prominent capsule of yellow fat; in the female the fat capsule is much less bulging.

Pyrrhomyias is like *Terenotriccus*, differing as follows. A-2R is divided; A-2L and A-3 are double, A-2L being wholly fused to A-3L. A-4 and A-5 are divided. A-5L and the ventral end of A-5R are fused to A-6. The pessulus is fused to the dorsal midline of A-6 and extends posteriad, then ventrad to the ventral region of A-3 where it is also fused. The internal cartilages are tapering bars, fused to A-3R and A-2L and extending posteriad to the level of B-1.

Myiobius is like *Terenotriccus*, differing as follows. In *M. atricaudatus* A-4 is complete and fused ventrally to A-5. The fusion includes A-4aR. The pessulus is absent, but its place appears to be taken by a broadened medial section of A-3L, occupying a midsagittal position. In *M. sulphurcipygius* A-4 and A-5 are incomplete dorsally and A-4 is fused to the ventral end of the pessulus.

Nuttallornis (Pls. 9 and 10) is unlike all of the above. A-1, A-2 and A-3 are divided; A-4 and A-5 are incomplete dorsally. A-4L and A-5L are fused at their dorsal ends. There is no pessulus. The internal cartilages are broad rounded triangles flexibly connected to the dorsal end of A-2 and to the cartilaginous plug. The latter forms a short wall at right angles to the sagittal plane.

Aphanotriccus is like *Nuttallornis*, differing as follows. A-4 and A-5 are complete and unfused. The internal cartilages are not attached to A-elements.

Empidonax is like *Nuttallornis*, differing as follows. The five species differ only in the details of A-elements. In six of the seven individuals A-1 through A-4 are divided and A-5 is complete. In the exception, YPM 700 (*E. minimus*), A-5 is incomplete dorsally, but the dorsal ends are in contact and closely fitted. In all specimens the dorsal ends of the divided elements are curled medially and adjacent elements are closely fitted. The pessulus is variable. In all except YPM 706 (*E. minimus*) and YPM 1544 (*E. oberholseri*) it is a short bar extending from between the dorsal ends of A-4 to the ventral end of that element, closely fitted to adjacent elements at the ends, but not fused. In YPM 706 the pessulus is lacking, but the dorsal ends of A-4 extend about one-third of the distance across the internal tympaniform membrane. In YPM 1544 A-5L has a posteriad and ventrad extension reaching halfway to the ventral part of the element. In all specimens the internal cartilages are J-shaped with the curvature directed ventrad. They are fused anteriorly to a small arched cartilaginous plug.

MacGillivray described the syrinx of *E. minimus* as being like that of *Tyrannus*, with two "dimidiate" (divided) elements, A-1 and A-2, and the rest of the A-elements complete. He found no pessulus. Maynard's description is not readily compared with others, as he provided no reference point. In his specimen the pessulus was present. In *E. traillii* Miskimen found A-4 and A-5 complete and fused, with the pessulus apparently fused to both ends of A-4.

Mitrephanes is like *Nuttallornis*, differing as follows. A-4 is incomplete dorsally and A-5 is complete. A substantial pessulus, mostly covered by a cartilaginous plug, is fused to A-4 ventrally and to A-5 dorsally.

Acchmolophus is like *Nuttallornis*, differing as follows. On my specimen there is an extra divided component on the right, which I will call A-2aR. Only A-4 is incomplete dorsally; A-5 and subsequent elements are complete. A-1 has a strong posteriad extension at the dorsal end, almost touching B-1. The dorsal ends of A-3L and A-4R extend posteriad and are fused together. There is no pessulus. The internal cartilages are straight bars, broadening in a slight T-shape at the posterior ends.

They are in contact at their anterior ends, in the interbronchial region.

Blacicus is like *Nuttallornis*, differing as follows. A-1 through A-4 are divided; A-5 and A-6 are incomplete dorsally. A-5L and A-6L are fused dorsally and jointly extend posteroventrad like a short pessulus, reaching about one-third of the way to their ventral ends.

Myiochanes is like *Nuttallornis*, differing as follows. A-1 through A-4 are divided; A-5 is complete and fused to the dorsal end of a thin pessulus. In the unnumbered specimen of *M. virens* there is an extra component, apparently A-1aR. The internal cartilages are thick bars attached anteriorly to a thin cartilaginous plug, which is fused to the dorsal ends of A-2.

The descriptions of this genus rendered by MacGillivray and by Maynard were too vague for close comparison with the above. MacGillivray stated that A-1 and A-2 were divided and the pessulus was absent, a statement he made of all tyrannids. Maynard did not describe the elements in detail. He found the pessulus present. Miskimen's description differs from the above in that both A-4 and A-5 are complete and that A-4, A-5, and A-6 are "incompletely fused." The pessulus apparently is attached to A-4 dorsally and ventrally.

Nesotriccus is unlike all of the above. A-1 is divided; A-2 and subsequent A-elements are complete. A-2 and A-3 are fused except for a small opening on each side of the dorsal midline. The pessulus is broad and is fused to A-2 at both ends. A pair of sheets of soft cartilage fills the spaces between the dorsal ends of B-1 and A-1 and between A-1 and the dorsomedial region of A-2. Short, pointed internal cartilages are attached to these sheets, adjacent to the dorsal ends of A-1.

Cnemotriccus is unlike all of the above. A-1 is divided. A-2 through A-7 are fused into a drum, slightly flared at the posterior end. The pessulus, laterally compressed, is fused to the drum at both ends. The internal cartilages are slightly rounded triangles floating in the membrane near the dorsal end of B-1.

Musculature.

Among the various species of *Myiarchus* (Pls. 9 and 10) there is considerable variation in the locations of muscle attachments and in the shapes of some muscles. The Mm. tracheolaterales either cover the entire ventral half of the trachea (*M. ferox, M. brachyurus, M. tuberculifer*) or have only a narrow space at the ventral midline (*M. crinitus, M. tyrannulus*). In YPM 1868 (*M. ferox*) a narrow slip from the left muscle crosses the ventral midline at A-11 and spirals across the surface of the right muscle to insert with the latter on the ventrilateral surface of A-6. A similar slip in YPM 2047 (*M. tyrannulus*) does not cross the right muscle but lies along its ventral edge to the insertion. M. tracheolateralis inserts on A-5 and A-6 in *M. crinitus* and *M. tuberculifer;* along a line from A-8 ventrally to A-6 laterally in *M. brachyurus;* and along a line from A-10 ventrally to A-6 laterally in *M. tyrannulus.*

M. sternotrachealis inserts directly on the lateral surface of the trachea, at the dorsal edge of M. tracheolateralis, the exact region of insertion being variable without apparent relation to species. The most posterior insertion is on A-11 through A-13 (*M. ferox*), the most anterior on A-15 through A-18 (*M. crinitus,* unnumbered specimen).

In *Myiarchus crinitus,* M. obliquus ventralis originates along the ventral midline on A-3 through A-6, as well as ventrilaterally on A-6 and laterally on A-5. In one

specimen (unnumbered) the area of attachment is nearly all on A-6, but in the other two the line undulates, resulting in the muscle having two heads. The attachment is continuous through the "dip" between the heads. The insertion is on the middle third of A-1 in all species. In *M. tuberculifer*, *M. brachyurus* and *M. tyrannulus* the lateral origin is a smooth line. In *M. ferox* there are three heads, but the "dips" between them are very shallow. The anterior limit of the midventral origin is on A-9 in *M. tyrannulus* and A-8 in *M. brachyurus;* in all others it is on A-6.

Müller's description and illustration of *M. ferox* differed from the above only in that M. tracheolateralis is narrow and lateral. In *M. stolidus* Maynard also found this muscle to be narrow. M. obliquus ventralis appears to be located much more laterally in *M. stolidus*, originating on A-5 laterally and inserting on the dorsal end of A-1. Miskimen described the Mm. tracheolaterales of *M. crinitus* as touching at the ventral midline. She found M. sternotrachealis inserting "on M. tracheolateralis" with some fibers continuous. Her statement concerning the presence of M. obliquus lateralis implied discontinuity in the origins of the muscle masses, but her description of the origins made them seem continuous. The difference between her two-muscled form and my one-muscled specimens appears to be a semantic one, but examination of a larger series of individuals may show that in some individuals or populations there is a discrete M. obliquus lateralis.

Eribates is like *Myiarchus crinitus*, differing as follows. M. tracheolateralis inserts on A-8 ventrally and on A-7 laterally. M. obliquus ventralis originates on A-4 through A-8 midventrally and on A-7 laterally.

Myiophobus is like *Myiarchus crinitus*, differing as follows. M. tracheolateralis covers the entire ventral surface of the trachea posterior to A-31 and inserts on A-6 only. M. obliquus ventralis originates ventrally on A-2 through A-6 and along A-6 to the dorsolateral surface. It inserts directly in A-1 and by a short narrow tendon to the dorsal end of B-1.

Cnemotriccus is like *Myiarchus crinitus*, differing as follows. The Mm. tracheolaterales converge ventrally at A-26 and insert on the anterior edge of A-7. M. sternotrachealis inserts directly on a narrow elliptical area from A-13 to A-18. M. obliquus ventralis originates along the ventral midline from A-4 to A-7 and laterally along A-7, directly posterior to the insertion of M. tracheolateralis. It inserts directly on the center of the A-1/B-1 membrane.

Nutallornis (Pls. 9 and 10) is unlike all of the above. The Mm. tracheolaterales converge at the level of A-12 and cover the ventral two-thirds of the trachea from there to their insertion on A-4 ventrally and on A-5 and A-6 laterally. Their fibers diverge around the insertions of the Mm. sternotracheales. The latter are asymmetrical. The right extends through *M. tracheolateralis* to insert in an elliptical area on the lateral surfaces of A-12 through A-15. The left divides into two fasciculi, a ventral one inserting like the whole right muscle, and a dorsal one inserting adjacent to the dorsal edge of M. tracheolateralis, on A-12 through A-16. The Mm. obliqui ventrales originate on a median raphe attached to the ventral ends of A-3 and to the midventral region of A-4 and A-5. The insertion is on the middle fifth of A-1. M. obliquus lateralis (absent in those genera described below as similar to this one) is a narrow band originating on the dorsolateral surface of A-6 and extending posteroventrally to insert on A-1, just dorsal to the insertion of M. obliquus ventralis.

Myiochanes is like *Nuttallornis*, differing as follows. M. tracheolateralis extends

further posteriad, inserting on A-2. A few lateral fibers insert on A-1. M. sternotrachealis divides into two fasciculi, a dorsal one extending through M. tracheolateralis to insert directly on A-12 through A-14 and a ventral one across the surface of M. tracheolateralis, inserting on the membranous sheath of that muscle. The raphe of M. obliquus ventralis attaches to A-2 through A-6. Its area of insertion on A-1 is longer than in *Nuttallornis.*

MacGillivray described *Myiochanes* as like *Tyrannus* and *Empidonax,* but his description was concerned only with generalities. Maynard's description is equally generalized. Miskimen's description differs from the above in several ways. In her specimens M. tracheolateralis inserted on A-6; M. sternotrachealis inserted ventrally "on M. tracheolateralis," with no dorsal insertion; M. obliquus ventralis was like the above, except that the origin was directly on the cartilaginous elements.

Empidonax is like *Nuttallornis,* differing as follows. The Mm. tracheolaterales are asymmetrical. As well as covering the left ventral quarter of the trachea, the left muscle extends about 15° to the right of the ventral midline. At the level of A-6 it divides into two fasciculi, one inserting midventrally on A-3 and A-4 and the other inserting laterally on A-1. In *E. difficilis* and *E. albogularis* some fibers insert ventrilaterally on A-5. The right muscle has only the lateral insertion. M. sternotrachealis inserts directly on the lateral surface of the trachea adjacent to the dorsal edge of M. tracheolateralis. The insertion is on A-10 through A-12 in *E. minimus;* on A-14 through A-17 in *E. flaviventris;* on A-12 through A-15 in *E. difficilis;* and on A-11 through A-15 in *E. albogularis* and *E. oberholseri.* M. obliquus ventralis originates on a median raphe continuous with the connective tissue between the ventral ends of A-2 and A-3. The raphe extends anteriorly to the level of A-6 but is not attached; at that level the raphe and its attached muscles overlie the left M. tracheolateralis. The insertion of M. obliquus ventralis is on the posterior edge of A-1.

MacGillivray's and Maynard's descriptions of *Empidonax minimus* are too superficial for close comparison with the above, although there are no points of disagreement. Miskimen's description of *E. traillii* differs in that she found M. tracheolateralis inserting on A-5, with a lateral extension to A-1; M. sternotrachealis inserting "on M. tracheolateralis," as well as directly on A-11 and A-12; the origin of M. obliquus ventralis direct, not by raphe.

Blacicus is like *Nuttallornis,* differing as follows. M. tracheolateralis inserts on A-2 ventrally and on A-1 laterally. M. sternotrachealis inserts directly on A-11 through A-13, adjacent to the dorsal edge of M. tracheolateralis. The raphe of M. obliquus ventralis is attached to the connective tissue between the ventral ends of A-3 and A-4 only. The muscle inserts along most of the ventral half of A-1.

Mitrephanes is like *Nuttallornis,* differing as follows. The Mm. tracheolaterales insert mainly on A-2 and A-3, with a few lateral fibers attached to A-13. M. sternotrachealis inserts directly on A-12 and A-13. The Mm. obliqui ventrales originate on a small piece of cartilage which, in turn, is attached to A-2 and A-3 on both sides of the ventral midline. This peculiar cartilage consists of a small triangular plate attached to the elements by two thin stalks. The two attaching stalks pass between the fibers of the Mm. tracheolaterales. The intrinsic muscle inserts on the middle third of A-1.

Aphanotriccus is like *Nuttallornis,* differing as follows. The Mm. tracheolaterales are separated by a midventral space of about 10° of tracheal circumference.

They insert on A-2. M. sternotrachealis inserts directly on A-13 through A-26, with about one-twentieth of the fibers continuous with M. tracheolateralis. The anterior tenth of the fibers of the Mm. obliqui ventrales are continuous between the pair. The insertion covers the ventral two-thirds of A-1, extending dorsally beyond the edge of M. tracheolateralis.

Aechmolophus is like *Nuttallornis,* differing as follows. The Mm. tracheolaterales insert on A-2, passing beneath the intrinsic muscles, and at their dorsal edges, on A-1. The Mm. sternotracheales insert on the ventrilateral surfaces of the Mm. tracheolaterales at the level of A-10 through A-12. The insertion of M. obliquus ventralis covers nearly the entire ventral half of A-1.

Nesotriccus is unlike all of the above. The Mm. tracheolaterales are quite narrow, each having a width of about 30° of tracheal circumference. They are separated ventrally by a space of about the same width. Their insertion is on A-3 ventrally and on A-2 and A-3 laterally. The right M. sternotrachealis inserts directly on A-8 through A-11, and also with about one-fifth of its fibers in continuity with M. tracheolateralis. The left muscle is similar, except that it reaches A-12 and has a narrow and extremely thin band of fibers extending across the ventral midline to insert on the surface of the right M. tracheolateralis. The band is probably an individual peculiarity of this specimen. Each of the Mm. obliqui ventrales originates adjacent to the ventral midline of A-2, A-3 and A-4. It extends laterally and posterodorsally to insert directly on A-1 (a few deep ventral fibers), by a broad thin tendon to the middle third of B-1 (a few superficial ventral fibers) and by a strong narrow tendon to the subterminal dorsal fifth of B-1 (the major part of the muscle).

Terenotriccus (Pls. 11 and 12) is unlike all of the above. M. tracheolateralis is narrow and ventrilateral, inserting directly on the ventral half of A-1, except the terminal sixth of the element. M. sternotrachealis inserts directly on A-10 through A-12, adjacent to the dorsal edge of M. tracheolateralis. There are no intrinsic muscles. Müller's description and illustrations agree closely with the above.

Pyrrhomyias is like *Terenotriccus,* differing as follows. The Mm. tracheolaterales converge ventrally at A-45 but diverge at A-11. A few fibers on the dorsal edge of each muscle are lightly attached to A-9 and A-10. The insertion is by a broad tendon to the middle third of B-1. The left M. sternotrachealis inserts on A-12 through A-15, the right on A-12 through A-14.

Myiobius is like *Terenotriccus,* differing as follows. The deep fibers of M. tracheolateralis are attached to A-5, so lightly that the connection was severed in dissection, without apparent damage to the muscle fibers. M. sternotrachealis inserts on A-11 through A-14.

Onychorhynchus is like *Terenotriccus,* differing only in that M. sternotrachealis is wholly continuous with the dorsal superficial fibers of M. tracheolateralis, which it touches at A-11.

SUBFAMILY PLATYRINCHINAE.

Specimens Examined.

Of 18 species in five genera, I have examined the following seven specimens of six species in three genera:

Platyrinchus mystaceus Vieillot
Platyrinchus cancrominus Sclater and Salvin
Tolmomyias sulphurescens (Spix), two specimens
Tolmomyias megacephalus (Swainson)
Rhynchocyclus olivaceus (Temminck)
Rhynchocyclus brevirostris (Cabanis)

I know of no descriptions by previous authors.

Cartilaginous Elements.

In *Platyrinchus* (Pls. 11 and 12) A-1, A-2, and A-3 are divided; A-4 is incomplete dorsally; A-5 and subsequent elements are complete. A large pair of internal cartilages extends from the dorsal end of the interbronchial region posteriad to the level of the dorsal end of B-1. The pair are thoroughly fused at their anterior ends, where they are also fused to a small bony disc lying on the dorsal midline. The dorsal ends of A-2 and A-3 are fused to the internal cartilages, but not those of A-1 and A-4. A narrow cartilaginous bar extends posteriad from the posterior end of each of the internal cartilages to the level of B-2, where it bends ventrad and extends nearly to the ventral edge of the internal tympaniform membrane. B-1 is more robust than the other B-elements and lacks the spatulate ends characteristic of them. There is no pessulus.

The two species of *Tolmomyias* are quite different from each other and from *Platyrinchus*. In *T. sulphurescens* (Pl. 20) A-1 is divided; A-2 and A-3 are double and fused along their medial sections. A-4 is incomplete dorsally and A-5 and the remaining A-elements complete. The pessulus is a mid-dorsal posteriad extension of A-5, bending ventrad and extending nearly to the ventral side. In one specimen (YPM C-244) the dorsal end of A-4L is fused to the pessulus. In the same specimen A-7 and A-8 are fused for their ventral halves. There is no fusion in YPM C-535. The internal cartilages are approximate triangles fused to the posterior medial edge of A-2. The B-elements are delicate, nonspatulate, and each except B-1 has an ossified cap on its middle third.

Tolmomyias megacephalus differs from *T. sulphurescens* as follows. A-1 through A-4 are divided and unfused. Due to shot damage some details of the mid-dorsal region are difficult to determine. The pessulus is present, but does not appear to be attached to A-5. There are two pairs of internal cartilages, a long dorsal pair fused to the dorsal ends of A-1 and extending posteriad to the level of B-5; and a ventral pair in the form of rounded squares floating in the membrane. B-1 is broader, thicker, and straighter than the other B-elements and lies very close to A-1.

Rhynchocyclus (Pls. 11 and 12) differs strongly from all of the above. In *R. brevirostris* A-1 through A-4 are divided and lie in planes tilted at about 45° to the tracheal axis. A-5 and subsequent elements are complete. A narrow mid-dorsal extension of the pessulus extends anteriad nearly to A-5. The internal cartilages consist of two pairs, both free. The dorsal pair is slender, slightly S-shaped, and extends from the region of the dorsal ends of A-2 to the ends of B-1. The ventral pair is shield-shaped and lies adjacent to the ventral ends of A-3. *R. olivaceous* differs from *R. brevirostris* in that A-1 is slightly softer, A-4 is double, and the pessulus extends to and is fused with A-5.

Musculature.

In *Platyrinchus mystaceus* M. tracheolateralis covers the ventral half of the trachea from about A-30 posteriad. It inserts by a very thin, transparent, broad tendon to A-1, just ventral of the center of the element. Some of the superficial lateral fibers of M. tracheolateralis are continuous with the ventral half of the M. sternotrachealis, which branches off from the trachea at A-12. The dorsal fibers of M. sternotrachealis insert on the lateral surfaces of A-15 through A-21. M. obliquus ventralis is very narrow, originating on the ventral surface of A-11, with a few fibers continuous with the deep lateral fibers of M. tracheolateralis. It extends posterodorsad to insert by a short narrow tendon on the dorsal tip of B-2. *P. cancrominus* is the same except that M. tracheolateralis inserts atendinously on A-1.

Rhynchocyclus differs sharply from *Platyrinchus*. M. tracheolateralis is a narrow band extending down the ventrilateral surface of the trachea, broadening slightly near its insertion, on A-3. M. sternotrachealis is robust (about one-third of the tracheal diameter) and inserts directly on an elliptical area on the lateral surfaces of A-5 through A-8 in *R. brevirostris* and A-6 through A-12 in *R. olivaceus*. M. obliquus ventralis originates on a median raphe attached to A-4 and A-5 in *R. brevirostris* and to A-5 and A-6 in *R. olivaceus*. It inserts directly in the middle of A-1 in both species.

The two species of *Tolmomyias* differ from all of the above and from each other. In *T. sulphurescens,* M. tracheolateralis consists of a narrow band on the lateral surface of the trachea, inserting on A-6 and A-7 on the left and A-7, A-8, and A-9 on the right. The line of its insertion follows closely the anterior edge of M. sternotrachealis. The latter inserts in a circular area on A-5, A-6, and A-7 on the left and A-6 through A-9 on the right. The single intrinsic muscle, which is most like M. obliquus lateralis of other genera, appears as a continuation of M. tracheolateralis, originating on A-5, at the posterior edge of M. sternotrachealis and extending posteriad to insert near the center of A-1.

In *Tolmomyias megacephalus* the Mm. tracheolaterales meet at the ventral midline at A-6. The insertion of each muscle is in three parts: the ventral half of the fibers inserts directly on A-4; the middle sixth of the fibers extends posteriad to A-2, where its insertion is beneath the intrinsic muscles; the dorsal third of the fibers inserts on the dorsolateral surface of A-5. M. sternotrachealis inserts directly on the lateral surfaces of A-11 and A-12 at the dorsal edge of M. tracheolateralis. M. obliquus ventralis originates on A-3 near the ventral midline and ventrilaterally on A-4 and extends posterolaterally to insert on A-1 just ventral to the center. M. obliquus lateralis originates dorsolaterally on A-5 and extends posteroventrally to insert on A-1, adjacent to the insertion of M. obliquus ventralis.

SUBFAMILY EUSCARTHMINAE.

Specimens Examined.

There are 77 species in the 25 genera recognized by Hellmayr (1927), to which I have added the two species of the genus *Corythopis,* usually included in the Conopophagidae. The inclusion of *Corythopis* in this subfamily is highly tentative, but it

certainly belongs in the Tyrannidae (see Ames et al., 1968). I have examined the following 28 individuals of 19 species in 15 genera:

Todirostrum cinereum (Linnaeus)
Todirostrum sylvia (Demarest), two specimens
Todirostrum plumbeiceps Lafresnaye
Oncostoma cinereigulare (Sclater)
Euscarthmornis margaritaceiventer (Lafr. and D'Orb.)
Lophotriccus pileatus (Tschudi), two specimens
Colopteryx galeatus (Boddaert)
Myiornis auricularis (Vieillot), two specimens
Hemitriccus diops (Temminck)
Pogonotriccus eximius (Temminck), two specimens
Leptotriccus sylviolus Cab. and Heine, two specimens
Phylloscartes ventralis (Temminck)
Capsiempis flaveola (Lichtenstein)
Euscarthmus melorhyphus Wied
Corythopis delalandi (Lesson), three specimens
Corythopis torquata Tschudi, two specimens
Pseudocolopteryx sclateri (Oustalet)
Pseudocolopteryx flaviventris (Lafr. and D'Orb.)
Habrura pectoralis (Vieillot), two specimens

I know of only the following descriptions by previous authors:

Todirostrum cinereum (Linnaeus) — Müller (1847, p. 36; 1878, p. 30)
Todirostrum poliocephalum (Wied) — Müller (1847, p. 36; 1878, p. 30)
Lophotriccus sp. — Müller (1847, p. 36; 1878, p. 30)
Colopteryx galeatus (Boddaert) — Müller (1847, p. 36; Pl. 4, figs. 1-3; 1878, p. 29)
Pogonotriccus eximius (Temminck) — Ames et al. (1968)
Corythopis delalandi (Lesson) — Ames et al. (1968)
Corythopis torquata Tschudi — Ames et al. (1968)

The description of the syrinx of *Corythopis* cited above was based on the dissections made in the present study.

Cartilaginous Elements.

In *Myiornis,* minor differences exist between the two specimens. In YPM 2727, A-1 and A-2 are divided; A-3 through A-7 are incomplete dorsally; A-8 and the remaining A-elements are complete, but in YPM 2725 A-3 is divided and A-8 and A-9 are incomplete dorsally. The pessulus in both specimens is a narrow flat plate, extending posteriad from between the ends of the most anterior dorsally incomplete element to the level of A-3, where it curves ventrad. The pessulus of YPM 2727 is fused midventrally to A-3; in YPM 2725, it is fused to the ventral end of A-3R. The B-elements are divided. The internal cartilages are nearly straight and are broadened, flattened, and slightly pointed at the posterior ends. Anteriorly they are flexibly attached to a transverse "horseshoe" of cartilage that partly encloses the pessulus.

Lophotriccus is like *Myiornis*, differing as follows. A-3 and A-4 are divided; A-5 through A-11 are incomplete dorsally. Both specimens are badly shot-damaged, obscuring the configuration of the internal cartilages. The tranverse "horseshoe" is absent. The pessulus is fused midventrally to A-5. The trachea from A-8 to the larynx is much enlarged, particularly in the dorsoventral direction. Its long diameter at A-24 is about 2.5 times that at A-8. Müller's description of the syrinx of *Lophotriccus* agrees with the above, except that in his specimen only A-5 through A-9 were incomplete dorsally.

Euscarthmornis is like *Myiornis*, differing as follows. A-1 through A-6 are divided; A-7 through A-13 are incomplete dorsally. The anterior part of the pessulus is mostly spongy white cartilage, with four irregularly shaped bony plates spaced between A-6 and A-13, varying in diameter from one to three times the width of the A-elements. The dorsal ends of A-1 through A-4 are fused to an inverted "V" of cartilage, continuous with the pessulus. The latter is fused midventrally to A-7.

Colopteryx (Pls. 13 and 14) is like *Myiornis*, differing as follows. A-1 through A-4 are divided; A-5 through A-12 are incomplete dorsally. The dorsal extension of the pessulus stops at the level of the A-10/A-11 membrane, but an additional bony plate lies between the dorsal ends of A-12. Müller's specimen was identical with the above except that the dorsally incomplete section extended through A-16 and the pessulus was continuous to A-16.

Hemitriccus is like *Myiornis*, differing as follows. A-1 through A-5 are divided; A-6 through A-14 are incomplete dorsally. The pessulus extends anteriad to the level of the A-7/A-8 membrane and is fused midventrally to A-6. The region between the dorsal ends of A-8 through A-14 is membranous, except for bony discs at the levels of the A-8/A-9, A-10/A-11 and A-11/A-12 membranes and of A-14. The dorsal ends of A-1 through A-4 are connected by an inverted "V" of cartilage.

Oncostoma is like *Myiornis*, differing as follows. A-1 through A-4 are divided; A-5 through A-22 are incomplete dorsally. The latter have only a slight turning-in at the dorsal ends. The mid-dorsal plate is about twice the width of the A-elements. Anterior to A-12 it is broken up into six sections which, although separate, are closely fitted at their edges. The pessulus is fused midventrally to A-4. There is no cartilage connecting the lower A-elements, nor are there any internal cartilages.

Habrura is unlike all of the above. A-1 is divided; A-2 is incomplete ventrally; A-3 and subsequent A-elements are complete. An extra divided component, A-3aR, is fused dorsally and ventrally to A-3. A-2 is very broad dorsally and blends imperceptably into a broad pessulus, which is narrow and free at its ventral end. In USNM 227218, A-3 is broadly fused dorsally to A-2. The internal cartilages are straight bars, flexibly fused to A-2 and extending posteriad to the level of A-2.

Capsiempis is like *Habrura*, differing as follows. The extra component is lacking. A-3 is connected to A-4 and A-4 to A-5 by narrow mid-dorsal sections. The internal cartilages taper to extremely thin sheets at their posterior ends, blending gradually into the surrounding membranes.

Pseudocolopteryx is like *Habrura*, differing as follows. The extra component is lacking. In *P. flaviventris* A-2 through A-4 are completely fused. In *P. sclateri* fusion has so obscured the edges of the elements that their number is uncertain. About five elements, A-2 through A-6, appear to be involved.

Pogonotriccus is unlike all of the above. A-1 through A-3 are divided; A-4 and subsequent elements are complete. The pessulus is a ventral continuation of a mid-dorsal plate which is fused to A-4 and to the dorsal ends of A-3. The internal cartilages are narrow, straight, tapering bars fused anteriorly to A-3 and extending posteriad to the level of A-1. Ames et al. provide an illustration (but no description) based on the two specimens described here.

Phylloscartes is unlike all of the above. A-1 and A-2 are divided; A-3 is double; A-4 and subsequent A-elements are complete. The medial sections of A-3 are fused for their ventral two-thirds and join the ventral surface of the element as a single narrow strip. A-2R is fused dorsally to A-3R. The internal cartilages are straight, narrow bars, fused to the dorsomedial regions of A-3.

Leptotriccus is unlike all of the above. A-1 and A-2 are divided. In YPM 2694, A-3 is divided; A-4 and subsequent elements are complete. In YPM 2693, A-3 is double; A-4 and A-5 are incomplete dorsally. In the first specimen the pessulus is a narrow bar fused to the mid-dorsal region of A-4 and extending about halfway to the ventral surface; in the second it is fused dorsally to A-4L and ventrally to both components of A-3. In the latter individual A-2R is fused dorsally to A-3R and the whole of A-5L to A-6. The internal cartilages in YPM 2694 are long rounded bars joined by a narrow neck to the dorsal ends of A-2; in YPM 2693 they are small hemispheres connected to A-2 by a narrow strand of cartilage.

Todirostrum (Pls. 11 and 12) is unlike all of the above. In *T. sylvia* A-1 through A-6 are divided; A-7 and subsequent A-elements are complete. In YPM 1070 the pessulus is a straight bar free at both ends; in YPM 1763 it is fused to A-6L at both ends. The divided A-elements extend about one-third of the way across the internal tympaniform membranes from the dorsal side and are fused to the dorsal internal cartilages, thin plates occupying the center thirds of the membranes. The ventral pair are small hemispheres attached to the ventral ends of B-2 and B-3. *T. cinereum* is like *T. sylvia,* except that only A-1 through A-4 are divided, the remaining A-elements being complete. A-5 and A-6 are fused about 30° to the left of the dorsal midline. *T. plumbeiceps* is like *T. sylvia* except that A-1 through A-5 are divided. Müller's descriptions of *T. cinereum* and *T. poliocephalum* agree with that of *T. cinereum,* above.

Euscarthmus is unlike all of the above. A-1 and A-2 are divided; A-3 and A-4 are incomplete dorsally; the remaining A-elements are complete. A-5 through A-9 are about twice the width of the other A-elements and are fused into a rigid cylinder (Pl. 20). The dorsal end of A-4L is fused to A-5. The pessulus is fused dorsally to A-3L, A-4L and A-5 and ventrally to A-4. The internal cartilages are straight tapered bars extending from the dorsal ends of A-3 to the level of B-2.

Corythopis is unlike all of the above. A-1 and A-2 are divided; A-3 and subsequent elements are complete. A-3 and A-4 are fused for about 15° on each side of the dorsal and ventral midlines, producing a short rigid drum. A robust pessulus, wide dorsally and narrow ventrally, is fused to A-3 at both ends. The internal cartilages are slightly flattened spheres lying in the internal tympaniform membranes at the level of B-4. Connecting each sphere with the respective dorsal end of A-2 are two narrow ribbons of cartilage, also lying in the membrane. B-1 is extremely heavy, its maximum width being about three times that of most A-elements. Its dorsal ends are slightly tapered and not flattened.

Musculature.

In *Oncostoma,* M. tracheolateralis is located on the ventrilateral surface of the trachea, inserting on A-10 and A-11. The lateral fibers are continuous with M. sternotrachealis. The whole of the latter muscle is continuous with M. tracheolateralis, which it meets at A-12. The right M. obliquus ventralis originates on A-9 and A-10 slightly to the left of the ventral midline and extends posterodorsad to insert in a narrow area near the dorsal end of B-1R. The left muscle originates on the right ventrilateral region of A-9 and A-10 and inserts near the dorsal end of B-1L. In the region of overlap each muscle divides into three layers which alternate, the deepest layer belonging to the right muscle, the most superficial to the left muscle. M. obliquus lateralis originates on the lateral surfaces of A-7 through A-9 and inserts on B-1 just dorsal to the insertion of M. obliquus ventralis.

Colopteryx (Pls. 13 and 14) is like *Oncostoma,* differing as follows. At A-15 M. tracheolateralis divides into two fasciculi, which extend dorsal and ventral to the insertion of M. sternotrachealis. The dorsal branch inserts on the dorsolateral surfaces of A-10 and A-11. The ventral fasciculus of the left muscle covers an area about 15° on both sides of the ventral midline and inserts in a narrow area on the ventral midline of A-5. The ventral fasciculus of the right muscle is much narrower than that of the left and inserts ventrilaterally on A-11. M. sternotrachealis inserts directly on the lateral surfaces of A-10 through A-15. M. obliquus ventralis originates ventrilaterally on A-10 and A-11 and extends superficial to the M. tracheolateralis. The number of layers in the region of crossing is difficult to determine, due to their thinness and the brittle quality of the fibers in my specimen. It appears to be about six for each muscle. M. obliquus lateralis originates on A-6 through A-8.

Müller's description and illustration of *Colopteryx* agree with the above except that he described a midventral azygous ("unpaariger") muscle which seems to correspond to the ventral fasciculus of the left M. tracheolateralis, but which is illustrated as being discontinuous with the rest of that muscle. The illustration shows the azygous muscle lying superficial to the Mm. obliqui ventrales.

Lophotriccus is like *Oncostoma,* differing as follows. M. tracheolateralis inserts on A-8 ventrilaterally and on A-5 dorsolaterally. M. sternotrachealis inserts on the lateral surfaces of A-7 through A-10. M. obliquus ventralis originates ventrilaterally on A-7 and A-8. In USNM 428193 the posterior fibers of the deepest muscle layer are continuous between the pair of muscles. M. obliquus lateralis originates laterally on A-6, immediately anteroventral to the insertion of M. tracheolateralis. Müller's brief description of *Lophotriccus* agrees completely with the above.

Euscarthmornis is like *Oncostoma,* differing as follows. The left M. tracheolateralis divides into three fasciculi. The ventral branch attaches midventrally to A-13, the middle one to the ventrilateral surfaces of A-8 and A-9, and the dorsal one to the dorsolateral surface of A-7 through A-9. Some superficial fibers of the middle fasciculus are continuous with those of M. sternotrachealis. In the right M. tracheolateralis the ventral branch inserts midventrally on A-14, beneath the subterminal part of the right muscle. The entire dorsal fasciculus is continuous with M. sternotrachealis. The Mm. sternotracheales insert only in continuity with the previous muscle. In the Mm. obliqui ventrales the deeper layers are situated more posteriorly. The combined

origins of the pair of muscles cover most of the ventral and ventrilateral surfaces of A-8 through A-11. M. obliquus lateralis originates on the lateral surfaces of A-8 and A-9 and inserts on B-1 just anterior to the insertion of M. obliquus ventralis.

Myiornis is like *Oncostoma,* differing as follows. M. tracheolateralis divides into two fasciculi which pass respectively ventral and dorsal to the insertion of M. sternotrachealis. The ventral fasciculus inserts on A-10 ventrally and on A-9 ventrilaterally; the dorsal one inserts on A-5 dorsolaterally. M. sternotrachealis inserts directly on the lateral surfaces of A-7 through A-13. The Mm. obliqui ventrales are asymmetrical. The left originates on both sides of the ventral midline of A-8 and ventrilaterally left on A-9 and A-10; the right originates on both sides of the ventral midline of A-9 and ventrilaterally right on A-10. The right muscle extends superficially across the left. Both muscles insert near the respective dorsal ends of B-1. M. obliquus lateralis originates on the lateral surface of A-6 and inserts on B-1, just dorsal to the insertion of M. obliquus ventralis.

Hemitriccus is like *Oncostoma,* differing as follows. The Mm. tracheolaterales are asymmetrical. The left muscle has three areas of insertion: on the dorsolateral surfaces of A-7 and A-8, in the center of B-1, and (crossing the ventral midline) on the ventral end of A-5R. The right muscle inserts only on A-7, A-8, and B-1. M. sternotrachealis inserts on a series of small areas on the lateral surfaces of A-9 through A-16. The insertion on each element extends ventrad a little further than that on the element posterior to it. M. obliquus ventralis is present on the left side only, originating midventrally on A-8 and inserting on B-1 just ventral to the attachment of M. tracheolateralis. M. obliquus lateralis originates on the dorsolateral surfaces of A-7 through A-13. There are only a few fibers attached to each element from A-9 through A-13, for they share the surface of the element with the fibers of M. sternotrachealis.

Habrura is unlike all of the above. The Mm. tracheolaterales converge at the level of A-10 and cover the ventral half of the trachea from there to their insertion on the anterior edge of A-3. M. sternotrachealis inserts directly on the lateral surfaces of A-8 through A-11. M. obliquus ventralis originates on the posterior edge of the ventral half of A-3 and inserts on the center of the A-1/B-1 membrane. M. obliquus lateralis is absent.

Capsiempis is like *Habrura,* differing as follows. M. tracheolateralis inserts on the ventral and ventrilateral surfaces of A-5. M. obliquus ventralis originates near the ventral midline of A-4 and A-5 and ventrilaterally on A-5. It inserts both on A-1 and on the A-1/B-1 membrane.

Phylloscartes is unlike all of the above. The Mm. tracheolaterales converge ventrally at the level of about A-26, covering the ventral surface of the trachea from there to their insertion, ventrally and ventrilaterally on A-4 and laterally on A-3. M. sternotrachealis inserts directly on the lateral surfaces of A-10 through A-14 adjacent to the dorsal edge of M. tracheolateralis. M. obliquus ventralis originates along the ventral quarter of A-4 and inserts in the center of the A-1/B-1 membrane. A narrow M. obliquus lateralis originates on the lateral surface of A-3 and inserts on the A-1/B-1 membrane, just dorsal to the insertion of M. obliquus ventralis.

Pseudocolopteryx is like *Phylloscartes,* differing as follows. M. tracheolateralis inserts on A-4 ventrally, on A-2 ventrilaterally and on A-4 laterally. M. sternotrachealis

inserts directly on A-13 through A-17. In addition, some of its anterior fibers are continuous with those of M. tracheolateralis. The Mm. obliqui ventrales originate on a midventral raphe attached to A-3 through A-5 and insert on the ventral third of A-1. M. obliquus lateralis originates on the lateral surface of A-4 and inserts on A-1, just dorsal to the insertion of M. obliquus ventralis.

Pogonotriccus is unlike all of the above. The Mm. tracheolaterales converge at about the level of A-27 and cover the ventral third of the trachea to their insertion on A-5. M. sternotrachealis inserts directly on the lateral surfaces of A-10 through A-14. M. obliquus ventralis originates on a raphe attached to A-4 and A-5 slightly to the right of the ventral midline. It inserts by a broad thin tendon to the dorsal end of B-1.

Euscarthmus is like *Pogonotriccus,* differing as follows. M. tracheolateralis inserts on A-3 ventrally and on A-2 ventrilaterally and laterally. M. sternotrachealis inserts on A-8 through A-13. The raphe of M. obliquus ventralis is attached to A-2 and A-3. The muscle inserts directly on the center third of B-1.

Leptotriccus is unlike all of the above. The Mm. tracheolaterales converge ventrally at the level of A-20 and diverge slightly at A-6 to insert ventrilaterally and laterally on A-3. M. sternotrachealis inserts adjacent to the dorsal edge of M. tracheolateralis on A-15 through A-21. M. obliquus ventralis originates on the ventral ends of A-2 (YPM 2694 only) and A-3, midventrally on A-4. It inserts near the center of the A-1/B-1 membrane. In YPM 2693 the posterior third of the fibers are continuous between the two muscles, without midventral attachment. M. obliquus lateralis originates on the lateral surface of A-3 and inserts on the A-1/B-1 membrane, just dorsal to the insertion of M. obliquus ventralis.

Todirostrum (Pls. 11 and 12) is unlike all of the above. M. tracheolateralis is a thin narrow, lateral muscle that divides into two fasciculi at the level of A-12 in *T. sylvia* and *T. cinereum* and A-11 in *T. plumbeiceps.* The fasciculi extend dorsal and ventral, respectively, to the insertion of M. sternotrachealis and insert on A-6 in *T. sylvia,* on A-7 in *T. cinereum,* and on A-5 in *T. plumbeiceps.* M. sternotrachealis inserts on A-8 through A-11 in *T. sylvia* and *T. cinereum,* and on A-7 through A-11 in *T. plumbeiceps.* The proper name for the intrinsic muscle is uncertain, but its position corresponds most closely to that of M. obliquus lateralis of other species. It originates laterally on A-6 in *T. sylvia,* on A-7 in *T. cinereum* and on A-5 in *T. plumbeiceps.* Its width at the origin is the same as that of the insertion of M. tracheolateralis in all specimens except YPM 1070 (*T. sylvia*), in which the intrinsic muscle is about one-third narrower, the difference being at the dorsal edge. It extends posteriad to insert on the center third of B-1.

Müller's description of *Todirostrum* is similar to the above except that he did not find an intrinsic muscle. He described M. tracheolateralis as extending to B-1.

Corythopis is unlike all of the above. The Mm. tracheolaterales converge ventrally at the level of A-14 and remain in contact to their insertion, on the ventral third of A-4. M. sternotrachealis is very thick, its diameter being about one third that of the trachea, and it inserts directly on the lateral surfaces of A-7 through A-10, adjacent to the dorsal edge of M. tracheolateralis. The Mm. obliqui ventrales originate on a median raphe attached to A-3 and A-4, slightly to the right of the ventral midline. Each muscle extends laterad and then posterodorsad to insert in the center of the A-1/B-1 membrane.

SUBFAMILY SERPOPHAGINAE.

Specimens Examined.

Of 25 species in 9 genera, I have examined the following 11 individuals of 7 species in 7 genera:

Tachuris rubrigastra (Vieillot), four specimens
Spizitornis parulus (Kittlitz)
Stigmatura budytoides (Lafr. and D'Orb.)
Serpophaga subcristata (Vieillot)
Inezia subflava (Scl. and Salv.)
Mecocerculus leucophrys (Lafr. and D'Orb.), two specimens
Colorhamphus parvirostris (Darwin)

I know of no descriptions by previous authors.

Cartilaginous Elements.

In *Serpophaga* A-1 is divided; A-2 and A-3 are double; A-4 and subsequent elements are complete. A-2 through A-5 are fused dorsally and A-3 and A-4 are also fused ventrilaterally, The fused medial sections of A-2 and A-3 form a continuous central plate. All of the B-elements are divided. The internal cartilages are narrow bars slightly curved dorsad, their anterior ends flexibly attached to the dorsomedial region of A-2 and to the dorsal end of A-1.

Spizitornis is like *Serpophaga,* differing as follows. A-2L and A-3L are fused laterally; A-3 and A-4 are broadly fused ventrally. The dorsal fusion of A-2 and A-3 and of A-3 and A-4 consists only of a narrow mid-dorsal region.

Mecocerculus is like *Serpophaga,* differing as follows. A-2 is divided and is fused to A-3 at its dorsal ends. The medial sections of A-3 are fused, forming a plate that is broad dorsally and narrow ventrally. A-5 is in contact with A-4 laterally but they are not fused. The internal cartilages are straight, are broader than those of *Serpophaga* and are constricted into a narrow neck near their attachment to A-2.

Colorhamphus is unlike all of the above. A-1 is divided; A-2 and subsequent elements are complete. A-2 and A-3 are joined by a narrow mid-dorsal plate. The pessulus is fused to A-2 at both ends. The internal cartilages are narrow rounded triangles flexibly attached to A-2 and extending posteriad to the level of B-1.

Inezia is unlike all of the above. A-1 and A-2 are divided; A-3 is double; A-4 and subsequent elements are complete. A-5 and A-6 are fused for about 15° on each side of the dorsal and ventral midlines. There is no pessulus. There are two pairs of internal cartilages. The usual dorsal pair are straight bars, fused to the dorsomedial region of A-3 and extend to the level of B-1, where they are flattened and terminally indented. The ventral pair are thin round discs fused to the ventrimedial region of A-3.

Tachuris (Pls. 13 and 14) is unlike all of the above. In three specimens (YPM 3, 2796, 2799) A-1 through A-3 are divided; A-4 and A-5 are incomplete dorsally; A-6 and subsequent elements are complete. YPM 4 differs only in that A-4 is divided. The dorsal ends of A-1 through A-5 are fused to an inverted "V" of soft white cartilage. There is no pessulus. In each internal tympaniform membrane is a large hemispherical capsule of yellow fat, lying on a thin disc of cartilage. The diameter of the capsule is about half that of the trachea.

Stigmatura is unlike all of the above. A-1 and A-2 are divided; A-3 through A-6 are incomplete dorsally; A-7 and subsequent elements are complete. A-7 and A-8 are fused for 60° to the right of the dorsal midline. The pessulus is fused to the posterior edge of A-7 and extends posteriad, bending ventrad at the level of A-4. Its ventral end touches A-3 but is free. A thin sheet of white cartilage connects the pessulus with the dorsal ends of A-2 through A-6. The internal cartilages are extensions of this sheet, terminating at the level of B-1. A-7 through A-10 have thickenings at the dorsal midline in line with the pessulus.

Musculature.

In *Serpophaga* the Mm. tracheolaterales converge ventrally at the level of A-19 and cover the ventral two-thirds of the trachea to their insertion, on A-3 ventrally, on A-4 ventrilaterally and on A-5 laterally. M. sternotrachealis inserts adjacent to the dorsal edge of M. tracheolateralis, directly on A-11 through A-16. M. obliquus ventralis originates immediately posterior to the insertion of M. tracheolateralis, on A-3, A-4, and A-5. It extends posterodorsally to insert along a narrow area in the middle of the A-1/B-1 membrane and on B-1, near the dorsal end.

Mecocerculus is like *Serpophaga,* differing as follows. M. tracheolateralis inserts on A-4 only. M. sternotrachealis inserts on A-11 through A-14. M. obliquus ventralis originates on A-4 only, and the direction of its fibers is posteriad. It inserts broadly in the center of the A-1/B-1 membrane.

Spizitornis is like *Serpophaga,* differing as follows. The Mm. tracheolaterales are separated ventrally by about 15° of tracheal circumference, except at their insertion on A-4, where they converge ventrally. M. sternotrachealis inserts on A-9 through A-12. M. obliquus ventralis originates on the ventral two-thirds of A-4 and extends posteriad to insert on the A-1/B-1 membrane very close to A-1.

Inezia is unlike all of the above. The Mm. tracheolaterales converge ventrally at about A-40. Near their insertion they form a single thick mass of fibers covering the ventral third of the trachea. They insert ventrally on A-2. M. sternotrachealis divides into two fasciculi near its insertion, the dorsal one inserting directly on A-10 and A-11, adjacent to the dorsal edge of M. tracheolateralis, the ventral one inserting on the membranous sheath of M. tracheolateralis. M. obliquus ventralis originates on a common median raphe which extends between the Mm. tracheolaterales to attach to A-4 and A-5. The insertion is on the dorsal third of B-1 by a broad thin tendon.

Stigmatura is like *Inezia,* differing as follows. M. tracheolateralis inserts on A-3. M. sternotrachealis inserts on A-19 through A-26. The raphe of M. obliquus ventralis attaches to A-3 and A-4 and the muscle inserts in the center of the A-1/B-1 membrane.

Colorhamphus is unlike all of the above. The Mm. tracheolaterales converge ventrally at A-36, becoming very thin. They become narrower and thicker as one muscle posteriorly and insert in a small midventral area of A-3. M. sternotrachealis inserts adjacent to the dorsal edge of M. tracheolateralis on A-11 and A-12. M. obliquus ventralis originates on A-2 near the ventral midline, and on A-3 just lateral to the insertion of M. tracheolateralis, extending posterolaterad to insert on the center of B-1.

Tachuris (Pls. 13 and 14) is unlike all of the above. The Mm. tracheolaterales converge ventrally at A-29 and remain in contact to their insertion. The ventral half of each muscle inserts ventrally on A-9 and A-10 (except in YPM 4, in which the

insertion is on A-10 and A-11). The dorsal half inserts directly on the middle of B-1. M. sternotrachealis inserts adjacent to the dorsal edge of M. tracheolateralis, on A-11 through A-17. M. obliquus ventralis originates on the ventral surfaces of A-8 and A-9 (on A-9 and A-10 in YPM 4) and extends posteriad parallel to and in contact with the dorsal fasciculus of M. tracheolateralis. It inserts on B-1 ventrally adjacent to the insertion of the latter muscle.

SUBFAMILY ELAENIINAE.

Specimens Examined.

Of 62 species in 16 genera, I have examined the following 33 individuals of 23 species in 12 genera:

Elaenia flavogaster (Thunberg)
Elaenia martinica (Linnaeus)
Elaenia albiceps (Lafr. and D'Orb.)
Elaenia chiriquensis (Lawrence), three specimens
Elaenia obscura (Lafr. and D'Orb.)
Elaenia fallax Sclater, two specimens
Elaenia gaimardi (D'Orbigny)
Elaenia viridicata (Vieillot)
Elaenia caniceps (Swainson)
Suiriri suiriri (Vieillot)
Suiriri affinis (Burmeister)
Sublegatus modestus (Wied)
Phaeomyias murina (Spix), two specimens
Camptostoma obsoletum (Temminck)
Camptostoma imberbe Sclater
Tyranniscus chrysops (Sclater), two specimens
Tyranniscus nigrocapillus (Lafresnaye)
Phyllomyias fasciatus (Thunberg)
Tyrannulus elatus (Latham)
Microtriccus semiflavus (Scl. and Salv.), two specimens
Leptopogon (species unknown), three specimens
Mionectes olivaceus Lawrence
Pipromorpha oleaginea (Lichtenstein), three specimens

I know of only the following descriptions by a previous author:

Elaenia flavogaster (Thunberg) — Müller (1847, p. 34; Pl. 3, figs. 11-13; 1878, p. 28)
Sublegatus modestus (Wied) — Müller (1847, p. 34; Pl. 3, figs. 16-18; 1878, p. 28)

Cartilaginous Elements.

Elaenia (Pls. 13 and 14) is typical of a number of genera. In *E. caniceps* A-1 is divided; A-2 and subsequent elements are complete. A-2 through A-4 are fused for their ventral halves and mid-dorsally, forming a rigid drum. The pessulus, which is about the same width as the A-elements, is fused to A-2 at both ends. The internal

cartilages are narrow bars attached anteriorly to A-2 and curved dorsad at the posterior ends. One specimen of *E. chiriquensis* (YPM 2021), *E. flavogaster, E. martinica, E. obscura, E. gaimardi,* and *E. viridicta* differ from *E. caniceps* in that A-2 is divided and free and the drum is composed of A-3 through A-5 wholly fused. In *E. fallax* the drum consists of A-3 and A-4. In *E. albiceps* and in two individuals of *E. chiriquensis* it consists of A-3 through A-6. Except in *E. caniceps* the internal cartilages are fused to A-2 and A-3. In all species except *E. chiriquensis* and *E. martinica* the posterior third of each internal cartilage extends ventrad in a thin semicircular sheet.

Müller's brief description of *E. flavogaster* mentioned only the lack of double elements and the presence of internal cartilages.

Suiriri is like *Elaenia caniceps,* differing as follows. A-2 is divided. In *S. affinis* the internal cartilages are tear-shaped plates connected to the dorsal ends of A-2 by narrow strips. In *S. suiriri* they are short broad "J's" with the free ends directed ventrad and the other ends attached as in *S. affinis.*

Phaeomyias is like *Elaenia caniceps,* differing as follows. In YPM 2038 the drum consists of A-2 and A-3, both of which are complete. In YPM 2046 there is no drum. A-2L is divided; A-2R and A-3 are double and A-2R and A-3R are fused ventrally and medially. The medial sections of A-3 are fused to the pessulus, which extends anterodorsally to join A-4 at the dorsal midline. In both individuals the internal cartilages are narrow, tapering posterior projections of thin sheets of soft cartilage which join the dorsal ends of A-1 and A-2.

Camptostoma is like *Elaenia caniceps,* differing as follows. The drum is completely fused and is deeply indented at the dorsal midline of A-2. The internal cartilages are short straight bars anteriorly fused to A-2 and bearing flat semicircular ventral extensions, like those of *Elaenia.*

Tyrannulus is like *Elaenia caniceps,* differing as follows. A-2 is fused to A-3 at the dorsal end only; A-3 and A-4 are fused for their ventral halves and at the dorsal midline. There are two pairs of internal cartilages. The dorsal pair are narrow, tapered bars fused anteriorly to A-2 and extending to the level of B-2. The ventral pair consists of circular discs fused to the ventral ends of A-1 and to the pessulus.

Microtriccus is like *Elaenia caniceps,* differing as follows. The drum consists of A-2 through A-5, completely fused. The pessulus is fused ventrally to A-2 and is closely fitted dorsally to the drum, but not fused. An extra divided component, A-6aR, is fused to A-6 at both ends. The internal cartilages are short narrow bars, slightly curved ventrad and fused anteriorly to A-2. Their ventral edges have flat semicircular extensions, similar to those of *Elaenia.*

Phyllomyias is unlike all of the above. A-1 is divided; A-2 is double; A-3 is divided; A-4 is incomplete ventrally; A-5 and subsequent elements are complete. The dorsal ends of A-3 extend ventrad parallel to the medial portions of A-2, about halfway to the ventral surface. A short narrow pessulus is fused dorsally to A-4 and extends ventrad about two-thirds of the distance to the ventral ends of that element. The internal cartilages are broad, thin plates fused anteriorly to A-2 and extending posteriad to the level of B-2.

Sublegatus is like *Phyllomyias,* as nearly as can be determined from the specimen at hand, in which the dorsal region from B-1 through A-3 is severely shot damaged. Müller's brief description of *Sublegatus* stated only that there is one double element and large internal cartilages.

Tyranniscus is unlike all of the above. In *T. chrysops* A-1 is divided; A-2 is double; A-3 is divided; A-4 is incomplete dorsally; A-5 and subsequent elements are complete. In YPM 922 A-5 and A-6 are fused; in YPM 2010 the left halves of A-4 and A-5 are fused and the dorsal end of A-3R is fused to A-2R. The pessulus is fused ventrally to A-4 and extends dorsally and anteriorly to A-5, to which it is also fused. In YPM 2010 the fusion also includes the left dorsal end of A-4. The internal cartilages are straight narrow plates fused to the dorsal end of A-2 and extending posteriad to the level of B-4. A narrow strip of cartilage joins the ventral ends of B-1 and B-2. *T. nigrocapillus* differs from *T. chrysops* in having A-2 divided; A-4 complete and wholly fused to A-5; the internal cartilages shorter, extending only to B-1 and bearing a ventrally directed fin; and B-1 not connected to B-2.

Leptopogon is unlike all of the above. A-1 and A-2 are divided; A-3 is incomplete dorsally; A-4 and subsequent elements are complete, except in AMNH 819, in which A-4 is incomplete dorsally and subsequent elements complete. The pessulus is free ventrally in all three individuals and is free dorsally in AMNH 820 and 821. In AMNH 819 it is continuous with the dorsal end of A-4. The internal cartilages are narrow (about half the width of the A-elements) and extremely thin. They extend from their attachment at A-2 to the level of B-4.

Pipromorpha (Pls. 13 and 14) is unlike all of the above. A-1 is divided; A-2 is double; A-3 and subsequent elements are complete. A-2 through A-6 are fused so completely that seams remain only laterally. The pessulus is an integral part of the drum, fused dorsally and ventrally to A-3 and medially to A-2, where lines of fusion are still visible. Each of the internal cartilages is a long blade extending posteriad from a flattened ball, which, in turn, is connected to A-2 by a narrow curved "stalk." The stalk comprises about one-third the total length of the cartilage, which extends posteriad to the level of B-7. The B-elements are all divided and differ from those of the above genera in that B-3 is the largest. The first three elements are enlarged at their ends; the remaining ones are unmodified.

Mionectes is like *Pipromorpha,* differing only in the form of the internal cartilages. They are identical in outline to those of *Pipromorpha,* but lack the ball at the anterior end of the blade.

Musculature.

In *Elaenia* (Pls. 13 and 14) there is considerable variation in the position of the Mm. tracheolaterales. In most species there is a midventral space of 15 to 45° of circumference, the widest being in *E. gaimardi.* In *E. chiriquensis* the pair are in contact from A-11 to their insertion and in *E. martinica, E. fallax, E. viridicata* and *E. caniceps* from about A-25 to their insertion. In all species the insertion is mostly on the anterior edge of the drum, the precise area being variable. In *E. chiriquensis* and *E. obscura* the ventral and lateral fibers attach to the anterior edge of the drum, while the middle part of the muscle extends to the ventrilateral surface of A-3. In all of the other species the ventral fibers extend further posteriad, to A-3 or A-2 and the insertion as a whole forms a spiral line to the lateral anterior edge of the drum.

M. sternotrachealis inserts directly on A-9 and A-10 in *E. flavogaster,* on A-10 through A-12 in *E. martinica,* on A-15 through A-19 in *E. albiceps,* on A-17 through A-24 in *E. chiriquensis,* on A-14 through A-17 in *E. obscura* and *E. fallax,* and on A-14 through A-16 in *E. caniceps.* In *E. gaimardi* the dorsal half of the fibers inserts

directly on A-13 through A-17 at the dorsal edge of M. tracheolateralis, while the ventral fibers are continuous with those of the latter. In *E. viridicata* there are three fasciculi: the posterior dorsal third of the fibers insert directly on A-13 and A-14; the anterior dorsal third are continuous with M. tracheolateralis: the ventral third insert on the midventral surface of the membranous sheath surrounding M. tracheolateralis.

The intrinsic musculature of *Elaenia caniceps* is typical of a number of species. M. obliquus ventralis originates on a raphe attached to the ventral midline of the drum and inserts by a broad tendon to the dorsal third of B-1. M. obliquus lateralis originates directly on the dorsolateral surfaces of A-4 and A-5 and along a line from there to the ventrilateral surface of A-2. It inserts directly on the middle third of A-1. *E. viridicata* differs from *E. caniceps* only in that the tendon of M. obliquus ventralis is very narrow. In *E. albiceps* the raphe of M. obliquus ventralis is attached to A-5 through A-7 and the muscle inserts on the A-1/B-1 membrane, near the middle of A-1. In *E. flavogaster, E. martinica, E. fallax,* and *E. gaimardi* the insertion is on the posterior edge of A-1. In *E. chiriquensis* and *E. obscura* the ventral muscle originates directly on the drum, adjacent to the ventral midline and ventrilaterally on A-5 and A-4, and inserts directly on the ventral third of A-1. M. obliquus lateralis originates on the lateral surfaces of A-5 and A-4 and inserts on A-1, dorsally adjacent to the insertion of M. obliquus ventralis. The origins of the two muscles are separated by the ventrilateral extension of M. tracheolateralis, except in one specimen of *E. chiriquensis,* in which the origins are continuous through a very narrow connecting region. Müller found M. obliquus ventralis inserting on A-1 in *E. flavogaster* but did not mention a second intrinsic muscle.

Camptostoma is like *Elaenia caniceps,* differing as follows. M. sternotrachealis inserts on A-10 and A-11. M. obliquus lateralis inserts on the middle of B-1 by a broad tendon extending beneath that of M. obliquus ventralis.

Suiriri is like *Elaenia caniceps,* differing as follows. The Mm. tracheolaterales are separated ventrally by about 20° of tracheal circumference. M. sternotrachealis inserts directly on A-11 through A-15, partly beneath the dorsal edge of M. tracheolateralis. In *S. affinis* the tendon and insertion of M. obliquus ventralis are broader than in *E. caniceps,* covering the dorsal half of B-1.

Phaeomyias is like *Elaenia caniceps,* differing as follows. The Mm. tracheolaterales are separated ventrally by about 15° of tracheal circumference. They insert on A-2 ventrally, on A-3 ventrilaterally, and on A-4 and A-5 laterally. M. sternotrachealis inserts on A-9 through A-13. The raphe of M. obliquus ventralis is attached to A-2 through A-4. The muscle inserts by a broad tendon in YPM 2046 but by a very narrow one in YPM 2038. M. obliquus lateralis originates on A-3 and A-4 ventrilaterally and on A-4 and A-5 laterally. In YPM 2046 the insertion is as in *Elaenia,* while in YPM 2038 some dorsal fibers of M. obliquus lateralis are attached to the tendon of M. obliquus ventralis.

Tyrannulus is like *Elaenia obscura,* differing as follows. M. tracheolateralis inserts on A-4 only, and M. sternotrachealis on A-11 through A-14. M. obliquus ventralis originates near the ventral midline of A-2 and A-3 as well as ventrilaterally and laterally on A-3 and A-4. It inserts in the center of the A-1/B-1 membrane. An M. obliquus lateralis is not separable from the ventral muscle, although the deep dorsal fibers are more anteroposteriorly oriented than the superficial ones.

Microtriccus is unlike all of the above. The Mm. tracheolaterales converge ventrally at about A-30 (variable) and cover the ventral half of the trachea from there to their insertion on A-5 ventrally and A-4 laterally. M. sternotrachealis inserts directly on the lateral surfaces of A-9 through A-12. M. obliquus ventralis originates directly on the drum, near the ventral midline of A-3 through A-5, and inserts in a small area near the dorsal end of B-1. M. obliquus lateralis is lacking.

The two species of *Tyranniscus* examined differ strongly from each other. *T. nigrocapillus* is like *Microtriccus,* differing as follows. M. tracheolateralis inserts on the entire ventral half of A-2. M. sternotrachealis inserts on A-11 through A-13. M. obliquus ventralis originates on a raphe attached midventrally to A-3 through A-5. It extends superficial to M. tracheolateralis to insert directly on B-1, near the dorsal end.

In *Tyranniscus chrysops* the Mm. tracheolaterales converge at A-33 and diverge again at the level of A-6. Each inserts directly in the center of the respective A-1/B-1 membrane. M. sternotrachealis inserts directly on the lateral surfaces of A-13 through A-18. There are no intrinsic muscles.

Leptopogon is unlike all of the above. The Mm. tracheolaterales converge ventrally, becoming narrower and thicker as one muscle and terminating in a blunt point at A-4. They insert by a pair of narrow tendons passing the raphe of the Mm. obliqui ventrales and attaching to the ventral ends of A-1 and B-1. At the level of A-2 the pair of tendons are connected by a short vinculum. The Mm. sternotracheales are variable among the three specimens. In AMNH 819 they insert directly on the lateral surfaces of A-5 through A-7; in AMNH 821 the ventral half of each muscle is continuous with M. tracheolateralis; in AMNH 820 the right M. sternotrachealis is wholly continuous with M. tracheolateralis, while the left inserts directly. M. obliquus ventralis originates on a raphe attached to the ventral midline of A-2 and A-3 and inserts near the dorsal end of B-1.

Phyllomyias is unlike all of the above. The Mm. tracheolaterales converge ventrally at the level of A-27. At A-4 each muscle divides into two fasciculi, a large ventral one inserting on A-3 and a small lateral one inserting on A-2. M. sternotrachealis also divides into two fasciculi. The dorsal branch inserts directly on the lateral surfaces of A-10 through A-16 and the ventral one on the membranous sheath surrounding M. tracheolateralis. M. obliquus ventralis originates on A-2 and A-3 near the ventral midline and extends laterad to insert near the center of the A-1/B-1 membrane.

Sublegatus is like *Phyllomyias,* but from the damaged specimen on hand one can only determine that M. sternotrachealis inserts as above and that M. tracheolateralis does not branch near its insertion. Müller mentioned only that M. obliquus ventralis inserted on B-1, and that the dorsal ["hintere," translated by Bell (Müller, 1878) as "posterior"] section of the syrinx is free of muscle.

Pipromorpha (Pls. 13 and 14) is unlike all of the above. The Mm. tracheolaterales converge ventrally at the level of A-37 and become narrower and thicker until, at their insertion on A-6, their combined width is about 30° of tracheal circumference. The majority of the resultant midventral muscle appears to consist of the left muscle. M. sternotrachealis inserts directly on the ventrilateral surfaces of A-11 through A-13. M. obliquus ventralis originates on A-6 immediately posterior to the

insertion of M. tracheolateralis and extends posteriad to insert on the ventral quarter of A-1 and, by a short tendon, on B-1.

Mionectes is like *Pipromorpha,* differing as follows. M. sternotrachealis is about twice as thick as that of *Pipromorpha,* its diameter being about one-third that of the trachea. The anterodorsal third of the muscle is continuous with M. tracheolateralis; the posterodorsal third inserts directly on A-7 through A-10; the ventral third inserts on the membrane surrounding M. tracheolateralis. The insertion of M. obliquus ventralis is by a broad tendon to B-1.

FAMILY OXYRUNCIDAE. SHARPBILL.

Specimens Examined.

I have examined one specimen of *Oxyruncus cristatus* (Gmelin), the only species in this family. The only previous description of the syrinx is that by Clark (1913, p.403), who noted only that the syrinx of *Oxyruncus* bore "a striking resemblance to *Sayornis* and *Tyrannus.*" He commented further that "the tongue and syrinx are so much like those of *Sayornis* that the only difference noted is that the tongue is a little more horny than in the Phoebe."

Cartilaginous Elements.

A-1 is a broad, divided element; A-2 is narrow, about half the width of A-1, and double; A-3, also narrow, appears to be divided, but has a long dorsomedial section; A-4 is wide and incomplete ventrally; A-5 and subsequent A-elements are complete. All of the B-elements are divided. A thick, narrow, slightly curved pair of internal cartilages is fused to A-2 and extends posteriad to the level of B-2. A narrow pessulus is fused dorsally and ventrally to A-4, which is indented where it meets the pessulus mid-dorsally.

Musculature.

The Mm. tracheolaterales broaden at about A-40 to cover the ventral half of the trachea. They converge ventrally so that at A-10, where the Mm. sternotracheales reach the trachea, the combined Mm. tracheolaterales cover only about 60° of tracheal circumference. They continue to converge and thicken until, at their insertion near the ventral midline of A-1 and A-2 (and on the connective tissue between the elements), the combined muscle mass is only about 30° wide. There is some connective tissue between the muscle and the ventral ends of B-1, but, due to the soft condition of the specimen, I am unable to determine whether or not this tissue is tendinous. Each M. sternotrachealis is wholly continuous with the dorsal edge of the respective M. tracheolateralis which it meets at A-10.

A conspicuous pair of intrinsic muscles, for which the name Mm. obliqui ventrales appears justified, originates on the ventral ends of A-3 and A-4, covered by the Mm. tracheolaterales. The intrinsic muscles extend posterolaterally, then posterodorsally, to insert on the center of B-1.

FAMILY PHYTOTOMIDAE. PLANTCUTTERS.

Specimens Examined.

Of the three species in the single genus, I have examined the following four specimens in two species:

Phytotoma rara Molina, two specimens
Phytotoma rutila Vieillot, two specimens

I know of only the following description by a previous author:

Phytotoma rara Molina — Kuchler (1936)

Cartilaginous Elements.

The two species examined are very similar. A-1 is divided. A-2 is complete in *P. rutila* and incomplete dorsally in *P. rara* (Pls. 17 and 18). In both species the posterior edge of A-2 is extended posteriad and is fused to the ventral end of the pessulus. In *P. rutila* the dorsal side is similar to the ventral one. In *P. rara* the dorsal end of A-2L extends posteriorly between the ends of A-1 and is fused to the dorsal end of the pessulus. A-3 and subsequent elements are complete. All of the B-elements are divided and are D-shaped in cross section. Only B-1, which lies very close to A-1, is spatulate at the ends. These findings agree closely with those of Kuchler.

Musculature.

The Mm. tracheolaterales are narrow, each covering about 30° of tracheal circumference. At the insertion of M. sternotrachealis, M. tracheolateralis divides into two fasciculi, the dorsal one inserting laterally on A-12 in *P. rutila* and on A-14 in *P. rara,* the ventral one inserting on the B-1/B-2 membrane, just posterior to the center of B-1. In one specimen of *P. rutila* the ventral tenth of the fibers insert on B-1. M. sternotrachealis inserts in an oval area on the lateral surfaces of A-10 through A-12 in *P. rutila* and A-11 through A-14 in *P. rara.* Kuchler described and illustrated M. tracheolateralis as inserting on the middle of B-1, but otherwise his findings agree with the above.

FAMILY PITTIDAE. PITTAS.

Specimens Examined.

Of 23 species in a single genus, I have examined the following four individuals of four species:

Pitta reichenowi Madarasz
Pitta boschi Müller and Schlegel
Pitta erythrogaster Temminck
Pitta atricapilla Lesson

I know of only the following descriptions by previous authors:

Pitta angolensis Vieillot — Garrod (1877)
Pitta cyanura (Boddaert) — Garrod (1877)
Pitta cyanoptera Temminck — Köditz (1925)
Pitta simillima Gould — Köditz (1925)
Pitta schwaneri Bonaparte — Köditz (1925)

Cartilaginous Elements.

All of the specimens examined are basically similar. In *Pitta reichenowi* (Pls. 17, 18) A-1 and A-2 are divided: there is an extra divided element A-2aR; A-3 and A-4 are incomplete dorsally; A-5 and subsequent elements are complete. There is no pessulus. The line of juncture of the two internal tympaniform membranes is oblique, extending from A-5 dorsally to A-3 ventrally.

P. boschi is like *P. reichenowi* except that A-3 is divided. In *P. erythrogaster* A-1 through A-4 are divided; A-5 and A-6 are incomplete dorsally; and there is no unpaired element. In *P. atricapilla* A-3 is incomplete dorsally and the unpaired divided element is A-3aR. A-4 and A-5 are complete and are fused ventrally.

In *P. angolensis,* Garrod found A-1 and A-2 divided. A-3 and A-4 were incomplete dorsally and fused. Although referring to the divided A-elements as "bronchial ring-segments," he noted that they appeared "like moieties of true tracheal rings." The pessulus was lacking and there was no extra element. In *P. cyanura* Garrod found A-1 through A-4 divided and A-5 and A-6 incomplete dorsally. The illustrations accompanying Garrod's text show four A-elements on the right and only three on the left, divided or incomplete. Although possibly an error on the part of the artist, the asymmetry in the drawing may well be accurate and Garrod's count based on the right side only.

Köditz' descriptions are in agreement with those of *P. erythrogaster,* above. In *P. cyanoptera* he found a short pessulus, lacking in the other two species examined by him.

Musculature.

The syringeal musculature appears to be essentially the same in all species of *Pitta.* M. tracheolateralis is narrow and lies on the ventrilateral surface of the trachea. It inserts on the ventrilateral surface of B-1. M. sternotrachealis is variable. In *P. reichenowi* it inserts directly on A-8 through A-10, at the dorsal edge of M. tracheolateralis; in *P. boschi* it inserts on A-9 through A-14. In *P. erythrogaster* and *P. atricapilla* M. sternotrachealis is wholly continuous with M. tracheolateralis.

The descriptions by Garrod and Köditz are in close agreement with *P. erythrogaster,* above.

FAMILY PHILEPITTIDAE. ASITIES AND FALSE SUNBIRDS.

Specimens Examined.

Of four species in two genera, I have examined the following two individuals, one of each genus:

Philepitta castanea (P.S. Müller)
Neodrepanis coruscans Sharpe

I know of only the following descriptions by previous authors:

Philepitta "probably *castanea*" — Forbes (1880b)
Neodrepanis coruscans Sharpe — Amadon (1951)

The specimen of *Neodrepanis* examined by me was the same individual as was studied by Amadon.

Cartilaginous Elements.

In *Philepitta* (Pls. 17 and 18) A-1 is incomplete dorsally. The right and left halves of the element are like the components of a divided element, lying in planes about 30° from the sagittal plane and joined at their ventral ends in a sharp point. The dorsal ends of A-1 are broadly spatulate. A-2 is complete and sharply folded around the dorsoventral axis. It is fused to A-1 for its ventral half. The pessulus is fused to A-2 at both ends. The remaining A-elements are complete and all of the B-elements are divided. B-1 and B-2 are very thin, straighter than the rest, and pointed at the ventral ends. Their straightness results in a narrowing of the tubes at that point.

Forbes' detailed description of *Philepitta* agrees closely with the above. He did not find fusion of A-1 and A-2, but noted that they were "closely apposed." The lateral view of the syrinx is inverted in Forbes' figure, but otherwise his illustrations closely approximate my specimen.

Neodrepanis (Pl. 20) is like *Philepitta,* differing as follows. The dorsal ends of A-1 are fused to A-2, but the ventral ends are free. A short triangular pair of internal cartilages are fused to the dorsal ends of A-1 and A-2. B-1 and B-2 are not modified as in *Philepitta;* they are as heavy and as curved as the other B-elements. Amadon's description of *Neodrepanis* was mainly concerned with the major points of comparison of this genus with *Philepitta* and did not go into detail.

Musculature.

The syringeal muscles of both genera are very simple. In *Philepitta* M. tracheolateralis is a broad lateral band, which divides into two fasciculi at the level of A-6. The fasciculi extend on the dorsal and ventral sides, respectively, of M. sternotrachealis and insert along nearly the entire length of A-1. M. sternotrachealis inserts in a roughly circular area on the lateral surfaces of A-5 and A-6. Near the insertion the fibers fan out beneath those of M. tracheolateralis. There are no intrinsic muscles. Forbes' description of the musculature of *Philepitta* agrees closely with the above.

Neodrepanis is like *Philepitta,* differing as follows. M. tracheolateralis is narrower, situated more ventrally, and does not divide into two fasciculi. Its insertion is along the ventral half of A-1. M. sternotrachealis inserts partly in continuity with the dorsal superficial fibers of M. tracheolateralis and partly on the membrane covering the ventral surface of the latter muscle.

FAMILY ACANTHISITTIDAE. NEW ZEALAND WRENS.

Specimens Examined.

Of the four species in this small family, I have examined the following two specimens:

Acanthisitta chloris (Sparrman)
Xenicus longipes (Gmelin)

I know of only the following description by a previous author:

Xenicus longipes (Gmelin) — Forbes (1882)

Forbes also mentioned very briefly the syrinx of *Acanthisitta chloris.*

Cartilaginous Elements.

In *Acanthisitta* (Pl. 19) the A- and B-elements are not as easily distinguished as in most other suboscines. The most anterior *free* divided element, which I have designated B-1, is thicker and narrower than that immediately anterior to it. Like the elements posterior to it, B-1 consists of a thick, ossified center section, about two-thirds of the total length of the element, and a soft, thinner section on each end. The first three B-elements are about half as wide as the remaining ones.

A-1 through A-4 are fused into a solid drum that bulges prominently in the lower ventral region and is indented at the ventral midline. A-1 is a divided element; A-2 is incomplete dorsally; A-3 and subsequent elements are complete. The seams between the fused elements are visible laterally and dorsally. The pessulus is firmly fused to the drum ventrally, where it is quite narrow. At its dorsal end the pessulus broadens and bends anteriad, forming a plate closely fitted between the ends of A-2 and just reaching A-3. Due to the age of the specimen, I was unable to determine whether or not the pessulus was fused to A-2R, as it was to A-2L.

Lying in the internal tympaniform membranes between the pessulus and the dorsal ends of B-4 is a pair of straight, narrow internal cartilages. At their anterior ends these cartilages are very close to, possibly even attached to, the pessulus.

Xenicus is almost identical to *Acanthisitta* in its syringeal cartilages, differing in having a drum of three elements (A-1 through A-3) and in lacking internal cartilages. Forbes' description and illustration of the syrinx of *Xenicus* agree closely with my specimen. He noted the close similarity of *Acanthisitta* to *Xenicus,* but did not mention internal cartilages.

Musculature.

In *Acanthisitta* the Mm. tracheolaterales are narrow for their entire length. Those fibers not continuous with the Mm. sternotracheales insert on the ventrilateral surfaces of A-2 through A-5. The posterior part of this pair of muscles is enclosed in a membranous sheath that becomes increasingly fibrous and silvery in color posteriorly, in the region between the muscles. The sheath ends at the level of A-3 and is lightly attached to the drum at that point. Laterally the sheath seems to be less aponeurotic. M. sternotrachealis inserts directly on the lateral surfaces of A-7, A-8 and A-9, with some anterior fibers continuous with those of M. tracheolateralis. There are no intrinsic muscles.

Xenicus is closely similar to *Acanthisitta*, differing only in that M. tracheolateralis inserts on A-6 and A-7, as well as in continuity with M. sternotrachealis. The latter, in addition to this continuity, inserts directly on A-5, A-6 and A-7. The sheath surrounding the lower trachea is more fibrous than in *Acanthisitta* and encloses both pairs of muscles down to the level of A-8.

Forbes' description of the syringeal muscles was concerned mainly with the absence of intrinsic muscles. He noted that in *Xenicus* there was a "thin lateral muscle terminating on the upper edge of the drum," presumably on A-3. The accompanying illustration, however, shows the muscle as terminating on the third or fourth element anterior to the drum, as it does in my specimen.

Suborder Menurae

family menuridae. lyrebirds.

Specimens Examined.

Of two species in the single genus, I have examined only the following individual:

Menura novae-hollandiae Latham (nestling)[1]

I know of only the following descriptions by previous authors:

Menura novae-hollandiae Latham — Eyton (1841b)
Menura novae-hollandiae Latham — Garrod (1876)

Cartilaginous Elements (see Pls. 17 and 18).

A-1, A-2 and A-3 are divided and are straighter than other A- or B-elements. A-1, the least curved, is narrow ventrally and broad dorsally, where it has a terminal posteriad projection. A-2, slightly more curved, is widest at the ventral end, where its width is about twice that of the dorsal end. A-3 is much narrower than the other two, more strongly curved around the tracheal axis, and fitted to A-4 but not fused. A-4 is complete and is bent at the dorsoventral axis. The pessulus is fused to A-4 at both ends. A-5 and subsequent elements are complete and similar to each other. Garrod reported the lower 16 complete elements to be anteroposteriorly compressed, describing them as "carinate . . . compressed from above downward." My specimen shows no such condition, but it is possible that the elements are modified as the individual matures.

A thick, fibrous syringeal aponeurosis extends from the esophagus, to which it is attached, to the trachea. It is attached to elements A-14 through A-24 and is continuous ventrally with the anterior wall of the interclavicular air sac. The aponeurosis is broad posteriorly but very narrow (about one-tenth of the tracheal diameter) in the region of A-3 through A-10. In this region it lies against the trachea in a slot between the Mm. bronchiales postici.

Musculature.

M. tracheolateralis extends down each side of the trachea to insert on the syringeal aponeurosis and on the lateral and dorsolateral surfaces of A-20 (dorsolaterally) through A-25 (laterally). M. sternotrachealis originates on the internal costal processes of the sternum and inserts on the lateral surfaces of A-6 through A-9.

There are three pairs of intrinsic muscles, which correspond closely to certain of the intrinsic muscles of the oscines. The names applied to the oscine muscles are therefore used here (see page 89).

M. bronchotrachealis anticus originates on the ventrilateral surfaces of A-24 and A-25 and on the posterior surface of the syringeal aponeurosis. It extends posteroventrad to insert subterminally on the ventral end of A-2.

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[1]Through the kindness of the Trustees of the Australian Museum, Sydney, I have examined the syrinx of an adult female *Menura novae-hollandiae* (one of two specimens in the collection of the Carnegie Museum). The syrinx of the adult differs from that of the nestling only in size. (Footnote added in galley proof.)

M. bronchotrachealis posticus originates on the dorsolateral surface of A-22 through A-24. It extends posteriad to insert on the dorsal end of A-1.

M. bronchialis posticus originates in a broad area on the dorsal and dorsolateral surfaces of A-14 through A-18 and on the posterior surface of the syringeal aponeurosis, near the dorsal midline. Its region of origin is anterolaterally continuous with that of M. bronchotrachealis posticus. M. bronchialis posticus inserts on the dorsal ends of A-2, A-3, and A-4.

The above description is in close agreement with Garrod's, differing only slightly in the insertions of the extrinsic muscles and the origins of the intrinsic muscles. Eyton's description is similar, except that M. bronchialis posticus has been omitted.

FAMILY ATRICHORNITHIDAE. SCRUB-BIRDS.

Specimens Examined.

Of the two species in this small Australian family I have examined the following:

Atrichornis clamosus (Gould)

The only previous description of the syrinx in this family appears to be the following, devoted to the other species:

Atrichornis rufescens (Ramsay) — Garrod (1876)

Cartilaginous Elements.

There are three heavy, divided A-elements, A-1 through A-3 (see Pl. 19). All are strongly curved around the tracheal axis. A-1, the heaviest of the three, has a robust posteriad extension at the dorsal end. A-2 is about twice as wide near the ventral end as at the dorsal end. There is a prominent ridge at the posterior edge of the ventral third of the element. A-3 is about the same width as A-2 at the dorsal end and tapers to a rounded point at the ventral end. A-4 is complete and extends posteriad midventrally to carry the pessulus, which is also fused to it mid-dorsally. A-4 and A-5 are fused mid-dorsally and are closely attached together by stiff connective tissue along their entire region of contact.

Garrod's description of *A. rufescens* mentions only that it "presents precisely the same arrangement as *Menura*." He noted the dorsal posteriad extension of A-1 and the ventral widening of A-2. These points do not show well in his illustration, but we may infer from his text that *A. rufescens* is similar to *A. clamosus* in its syringeal cartilages.

Musculature.

The Mm. tracheolaterales widen dorsally until at their insertion they cover the entire dorsal two-thirds of the trachea with a thin sheet of muscle which is somewhat thicker at its ventral edge. The insertion is on the anterior surface of the syringeal aponeurosis and on the underlying elements, A-13 through A-17.

M. sternotrachealis originates on the lateral edge of the internal surface of the coracoid process of the sternum and inserts on the lateral surfaces of A-4 and A-5.

There are three well-developed pairs of intrinsic muscles, the positions of which correspond so well to those of certain muscles of the oscine syrinx that the use of

the same names appears warranted. (For a description of the oscine muscles, their nomenclature and synonymy, see p. 89). M. bronchotrachealis anticus originates ventrally and ventrilaterally on the aponeurosis, ventrilaterally on A-13 through A-16, and, along its medial edge from A-4 (where the members of the pair are almost in contact), through A-16. The medial fibers of this muscle are short and occupy essentially the same position as does M. bronchialis anticus pars medialis in most oscines. In *Atrichornis,* however, there is complete continuity of origin and of insertion in this muscle mass, so the naming of the short medial fibers as a separate muscle does not seem warranted.

M. bronchotrachealis posticus originates on the posterior surface of the aponeurosis and on adjacent areas of A-12 dorsally through A-15 laterally. It inserts on the dorsal ends of A-3 and A-4. The muscles of this pair are in contact at the dorsal midline from origin to insertion.

A long, substantial M. bronchialis posticus lies posteroventral to M. bronchotrachealis posticus, originating on the ventrilateral surfaces of A-5 through A-9 and inserting on the dorsal ends of A-1 and A-2 and on the connective tissue between them.

The above differs substantially from the description by Garrod that has served for nearly a century as the basis for the belief that *Atrichornis* possesses only two pairs of intrinsic muscles. He described a long dorsal muscle originating on the aponeurosis and inserting on the dorsal end of A-1. He also noted the presence of the long ventral muscle but did not mention any fibers originating along the medial edge. Garrod did not find any muscle to correspond to M. bronchialis posticus, but it might have been overlooked due to poor preservation or inadequate magnification. In his illustration there is clearly a space in the region occupied in *A. clamosus* by M. bronchialis posticus.

Suborder Passeres ("Oscines")

NOMENCLATURE.

The nomenclature employed for the previous suborders is used for the oscines, with the following modifications.

Cartilaginous Elements (Pl. 21).

The oscine syrinx is characterized by the presence of a drum formed by the fusion of three or four complete elements. Posterior to the drum are three divided elements often known as "intermediary bars" (Owen, 1866) or "bronchial bars" (most other European authors). These elements are heavy and bony, round or slightly flattened in section, and concave posteriorly or straight. Posterior to them are other divided elements which are slender, wholly or partly cartilaginous, round or D-shaped in section, and slightly concave anteriorly.

The interrelationships of the oscine syringeal elements have always been controversial and at least four different nomenclatures have been used (Table 3). MacGillivray (1839) considered the "intermediary bars" to be tracheal elements, numbering them anteriad in continuity with the drum (which he considered a single element) and other complete elements. Owen (1866) treated the "bars" as neither tracheal nor bronchial, numbering them anterior to posterior. He numbered the "tracheal rings" anteriad from the element nearest the drum, leaving the latter unnumbered. Elements posterior to the "intermediary bars" were designated "bronchial

semirings" and numbered from anterior to posterior. Wunderlich (1886), in a system followed by most subsequent European authors, treated all divided elements as "bronchial bars" or "semirings," numbering them posteriad from the one closest to the drum. Complete elements were numbered anteriad, starting with the one anterior to the drum. Miskimen (1951) followed Owen's system, except that she reversed the numbering of the intermediary bars.

TABLE 3. Synonymy of syringeal cartilages in the suborder Passeres.

Ames, modified from MacGillivray, 1839	Owen (1866)[1]	Miskimen (1951)[2]	Wunderlich (1886)[3]
A-9	Tracheal ring II	Tracheal ring II	Tracheal ring II
A-8	Tracheal ring I	Tracheal ring I	Tracheal ring I
A-7, A-6, A-5, A-4	Drum	Drum	Drum ("Trommel")
A-3	Intermediary Bar I	Intermediary Bar III	Bronchial Bar I
A-2	Intermediary Bar II	Intermediary Bar II	Bronchial Bar II
A-1	Intermediary Bar III	Intermediary Bar I	Bronchial Bar III
A-1/B-1 Membrane	External tympaniform membrane		
B-1	Bronchial semiring I	Bronchial semiring I	Bronchial semiring IV
B-2	Bronchial semiring II	Bronchial semiring II	Bronchial semiring V
B-3	Bronchial semiring III	Bronchial semiring III	Bronchial semiring VI

[1] This method was also used by Shufeldt (1890).
[2] This method was also used by Berger (1957).
[3] This method was also used by Fürbringer (1888), Gadow and Selenka (1893), Haecker (1900), Setterwall (1901) and Köditz (1925).

Precise evolutionary or developmental homology between the "intermediary bars" of the oscines and the lower A-elements of other suborders is difficult to confirm, but there is much to suggest a close relationship. The shape and composition of the bars correspond to those of A-elements, while the configuration of the divided elements posterior to the bars is more like that of the B-elements. Moreover, the bars are closely fitted to each other and the most anterior of them lies in a groove in the edge of the drum. Authors who have considered the bars as part of a bronchial series have also recognized the disjunct nature of the series in naming the membrane between the posterior bar and the next posterior element, the Membrana tympaniformis externa.

In the following descriptions I utilize the concept held by MacGillivray (1839) that the "intermediary bars" and the drum are part of a natural series continuous with the anterior complete elements. The similarity of this series to those of many members of other suborders urges the use of the "A" and "B" designations employed elsewhere. Among the large variety of syringeal patterns in the Tyranni are several that closely approach the oscine configuration structurally, the closest that I have examined being that of *Elaenia chiriquensis*.

Musculature.

The intrinsic syringeal muscles of the Passeres have been described with more than a dozen systems of nomenclature (Table 4). Conceptural differences regarding what constitutes a single muscle have led to various figures for the total number of oscine muscles. The disagreement centers upon two questions: 1) whether muscles should be named on the basis of function or of location, and 2) whether a single mass of muscle fibers attached to several cartilaginous elements constitutes one muscle or several. My choice of Owen's (1866) nomenclature is based on its applicability to a large number of oscine syringeal patterns, rather than on concepts.

Savart (1826) named four pairs of muscles in *Corvus* on the basis of their action on individual cartilages. His system was not used by any subsequent author. Owen (1866) provided the simplest of the several nomenclatures used by recent authors, recognizing five pairs of intrinsic muscles. In an unfortunate attempt to homologize the axes of the avian body with those of man he named ventral muscles "anticus" and dorsal ones "posticus." Wunderlich (1886) named seven pairs of muscles on a functional basis. Using the positions of the muscles, Fürbringer (1888) named eight pairs, to which Mayr (1931) added a ninth. Setterwall (1901), basing his system on muscle positions, produced a wholly different nomenclature, also with eight muscles. Köditz (1925) combined the systems of Fürbringer and Setterwall, recognizing eight pairs of muscles, one of which is not synonymous with any of those named by his predecessors. Köditz was the only author whose nomenclature was not based on a corvid (*Corvus* or *Pica*), hence the difference in application.

With the exception of Owen's, each of the above systems requires the addition of many new names to be applicable to all the oscines. Until more is known about the operation of the syrinx it seems unwise to name the muscles on a functional basis or to employ functional groupings of muscle fasciculi. I have modified Owen's nomenclature by the merger of two dorsal muscles and the recognition of two parts to one of the ventral muscles, resulting in the following system.

The extrinsic muscles are the same as in the other suborders: M. tracheolateralis and M. sternotrachealis.

The following four pairs of intrinsic muscles are recognized:

1) M. bronchotrachealis posticus originates dorsally and dorsolaterally on the syringeal aponeurosis and on the elements immediately posterior to the attachment of the aponeurosis. It extends posteriad to insert on the dorsal ends of A-1, A-2, and/or sometimes A-3, with some fibers attached to the connective tissue between the elements. The medial portion of M. bronchotrachealis posticus was treated by Owen as M. bronchotrachealis brevis, but in view of the frequent continuity of origin and insertion the two are best treated as one muscle.

2) M. bronchotrachealis anticus is the ventral counterpart of M. bronchotrachealis posticus, originating ventrilaterally on the syringeal aponeurosis and on the elements posterior to it, and extending posteriad to insert on the ventral end of A-1 and/or A-2.

3) M. bronchialis posticus is a short deep muscle on the dorsolateral surface of the syrinx, originating on the lateral surface of the drum and/or on the elements immediately anterior to the drum. It extends posterodorsally to insert on the dorsal end of A-1 (sometimes also on A-2) immediately ventral to the insertion of M. bronchotrachealis posticus.

TABLE 4. Synonymy of syringeal muscles in the suborder Passeres.

Owen (1866) Shufeldt (1890) Miskimen (1951) Ames, modified.	Wunderlich (1886)	Gadow and Selenka (1893) Fürbringer (1888) Haecker (1900)	Setterwall (1901)	Köditz (1925)
Corvus corax or *brachyrhynchos*	*Pica pica*	*Corvus corone*	*Pica pica*	*Pycnonotus, Irena.*
M. broncho-trachealis anticus	M. levator longus anterior arcus secondi	M. tracheo-bronchialis ventralis	M. ventralis longus	M. laryngo-syringeus ventralis (longus)
M. broncho-trachealis posticus	M. levator longus posterior arcus secondi	M. tracheo-bronchialis dorsalis longus	M. dorsolateralis longus	M. laryngo-syringeus dorsolateralis
M. broncho-trachealis brevis. (I do not feel that this muscle is separable from the preceding.)	M. tensor membranae tympaniformis internae	M. tracheo-bronchialis dorsalis brevis	M. dorsalis longus	M. laryngo-syringeus dorsalis
		M. syringeus dorsalis	M. dorsalis brevis	M. syringeus dorsalis (brevis)
M. bronchialis posticus	M. levator brevis posterior arcus secondi	M. syringeus dorsolateralis	M. dorsolateralis brevis	M. syringeus dorsolateralis (brevis)
		M. interbronchialis lateralis (Mayr, 1931)		
M. bronchialis anticus, pars medialis	M. rotator arcus tertii	M. tracheo-bronchialis obliquus	M. ventrilateralis brevis externus	M. laryngo-syringeus ventrilateralis (longus)
pars lateralis	M. levator brevis anterior arcus secondi	M. syringeus ventralis	M. ventralis brevis	M. syringeus ventrilateralis externus (brevis externus)
	M. laxator membranae tympaniformis externa	M. syringeus ventrilateralis	M. ventrilateralis brevis internus	M. syringeus ventrilateralis internus (brevis)
M. sternotrachealis	M. sterno-trachealis	M. tracheo-clavicularis	not mentioned	M. sternotrachealis

4) M. bronchialis anticus occupies the ventral and ventrilateral regions of the syrinx, originating on the anterior edge of the ventral and ventrilateral surfaces of the drum, and sometimes on the elements anterior to the drum. More often than not the muscle has the following two well-differentiated fasciculi:

pars medialis. Most of this fasciculus originates ventrally on the medial side of M. bronchotrachealis anticus. The insertion is on the ventral end of A-2, sometimes also on A-3. The pars mediales of the two muscles may be in contact at the ventral midline or widely separated.

pars lateralis. This fasciculus originates lateral to the origin of the pars medialis, usually in continuity with the latter. It extends posteroventrad to insert near the ventral end of A-1 just dorsal to the insertion of M. bronchotrachealis anticus.

The fasciculi of M. bronchialis anticus may appear as two muscles with separate origins and insertions, as a single band with continuous origin and insertion, or as one of any number of intermediates.

THE OSCINE SYRINX, EXEMPLIFIED BY *CORVUS*.

Specimens Examined.

The genus *Corvus* is described as typical because it represents the syringeal structure of a large majority of oscines, because it is readily available to most anatomists, and because it has been the basis for most previous systems of nomenclature. I have examined the following 16 specimens of four species of *Corvus* and one species of *Pica:*

Corvus brachyrhynchos Brehm, 11 specimens
Corvus corone Linnaeus
Corvus macrorhynchos Wagler
Corvus ruficollis Lesson
Pica pica (Linnaeus), two specimens

I know of the following descriptions by previous authors:

Corvus brachyrhynchos Brehm — MacGillivray (1838)
Corvus brachyrhynchos Brehm — Maynard (1926)
Corvus brachyrhynchos Brehm — Miskimen (1951)
Corvus brachyrhynchos Brehm — Chamberlain et al. (1968)
Corvus corax Linnaeus — Yarrell (1833)
Corvus corax Linnaeus — Owen (1866)
Corvus corax Linnaeus — Fürbringer (1888)
Corvus corax Linnaeus — Haecker (1900)
Corvus corone Linnaeus — MacGillivray (1839)
Corvus corone Linnaeus — Gadow and Selenka (1893)
Corvus corone Linnaeus — Mayr (1931)
Pica pica (Linnaeus) — Wunderlich (1886)
Pica pica (Linnaeus) — Setterwall (1901)

Cartilaginous Elements.

The A-elements of *Corvus* (Pl. 21, figs. 3 and 4) consist of three divided elements (A-1 through A-3), a drum of four wholly fused complete elements (A-4 through A-7), and the remaining unmodified complete elements. A-1 is straight, except for

the dorsal third, which is bent slightly posteriad. It is dorsoventrally oriented. A-2 is concave posteriorly, especially at the ventral end, and is round in cross section except at the ends, which are spatulate. A-3 is closely fitted to the posterior edge of A-4 for its full length.

A-4 through A-7 are complete elements wholly fused into a drum. In most individuals the outlines of the original elements are visible. The pessulus is fused to A-4 at both ends. It is triangular in cross section and bears a small anteriorly directed vane, the Membrana semilunaris.

All of the B-elements are divided and lie in planes perpendicular to the bronchial axes. Each has an ossified cap covering the center third of the element.

All of the previous descriptions of corvids agree with the above in the essential points, except those by MacGillivray (1838, 1839). He described only the last two "tracheal" elements as divided ("dimidiate") yet from his muscle descriptions the two divided elements are plainly A-1 and A-2. Apparently MacGillivray believed A-3 to be part of the drum, to which it is attached with dense fibrous connective tissue. Chamberlain et al. (1968) found that the drum in their specimens (55 in number) comprised five elements. The basis for this apparent variation needs further investigation.

Musculature.

The syringeal muscles of *Corvus* are, for the most part, distinct from one another at their edges.

M. tracheolateralis covers the dorsal two-thirds of the trachea, inserting on the syringeal aponeurosis and on elements A-10 laterally, A-9 dorsolaterally, and A-8 and A-7 dorsally.

M. sternotrachealis originates on the inner surface of the coracoid process of the sternum and inserts on the lateral surfaces of A-8 and A-9.

M. bronchotrachealis posticus originates on the posterior surface of the syringeal aponeurosis and on A-11 laterally, A-10 dorsolaterally and A-9 and A-8 dorsally. It extends posteriad, covering the dorsal surface of the trachea in a thin sheet and inserts on the dorsal ends of A-2 and A-3, and on the connective tissue between the two elements and between A-3 and A-4. The two Mm. bronchotracheales postici touch at the dorsal midline.

M. bronchotrachealis anticus originates on the posterior surface of the syringeal aponeurosis, ventrally adjacent to the origin of M. bronchotrachealis posticus, and on the ventrilateral surfaces of A-13 and A-12. It extends posteriad to insert on the ventral ends of A-1 and A-2.

M. bronchialis posticus originates on A-7 and A-8 laterally and on A-7 dorsolaterally. It extends posterodorsally to insert on the dorsal ends of A-2 and A-3 just ventral to the insertion of M. bronchotrachealis posticus.

M. bronchialis anticus has two well-differentiated fasciculi. They are in contact at their origins but separate at insertion. The pars medialis originates on the ventral surface of A-7 and on the ventrilateral surface of A-8. It extends posteriad on the medial side of M. bronchotrachealis anticus and beneath the latter muscle, to insert on the ventral end of A-2. The pars lateralis originates on the lateral surface of A-8 immediately posterior to the insertion of M. sternotrachealis. It extends posteriad, superior to the insertion of M. bronchialis posticus, and inserts on A-1 immediately dorsal to the insertion of M. bronchotrachealis anticus.

TABLE 5. Numbers of individuals, species, and genera of the suborder Passeres examined in this study.

Family	Out of a total of:		I have examined:		
	SPECIES	GENERA	SPECIMENS	SPECIES	GENERA
Alaudidae	76	15	15	9	6
Hirundinidae	78	19	21	16	11
Campephagidae	69	9	8	8	6
Dicruridae	20	2	6	4	2
Oriolidae	26	2	4	4	2
Corvidae	100	26	31	17	13
Cracticidae	10	2	2	2	2
Grallinidae	4	3	2	2	2
Ptilonorhynchidae	18	8	2	2	2
Paradiseidae	43	22	2	2	2
Paridae	65	9	5	5	4
Hypositidae	1	1	1	1	1
Sittidae	17	3	13	10	3
Certhiidae	17	5	6	3	3
Chamaeidae	1	1	1	1	1
Timaliidae	251	64	32	31	21
Paradoxornithidae	12	2	3	3	2
Pycnonotidae	120	15	19	18	8
Chloropseidae	14	3	5	4	3
Cinclidae	4	1	2	2	1
Troglodytidae	59	14	13	9	7
Mimidae	27	13	9	9	8
Turdidae	307	48	67	59	26
Zeledoniidae	1	1	1	1	1
Sylviidae	398	85	51	50	32
Regulidae	5	1	4	2	1
Muscicapidae	328	56	45	45	27
Prunellidae	11	1	4	3	1
Motacillidae	48	5	5	4	2
Bombycillidae	4	2	5	2	1
Ptilogonatidae	4	3	3	3	3
Dulidae	1	1	4	1	1
Artamidae	10	1	3	3	1
Vangidae	12	8	8	8	6
Laniidae	65	10	10	10	7
Prionopidae	9	2	5	5	2
Cyclarhidae	2	2	1	1	1
Vireolaniidae	2	2	1	1	1
Callaeidae	3	3	none	—	—
Sturnidae	109	26	27	24	15
Meliphagidae	160	65	13	13	11
Nectariniidae	105	5	4	4	4
Dicaeidae	54	7	4	4	3
Zosteropidae	80	10	8	8	4
Vireonidae	37	4	5	5	3
Coerebidae	36	12	4	4	4
Drepanididae	22	9	7	7	5
Parulidae	119	18	21	20	14
Ploceidae	313	40	11	4	4
Icteridae	94	35	12	7	6
Tersinidae	1	1	1	1	1
Thraupidae	222	61	18	16	14
Catamblyrhynchidae	1	1	none	—	—
Fringillidae	412	120	61	55	48
TOTALS	4007	884	615	533	359

When allowance is made for differences in nomenclature, most of the previous descriptions agree with the above. An exception is the work of Gadow and Selenka (1893), but the disagreement stems from errors in the illustrations. Comparison of the three views of the oscine syrinx (figs. 62-64) with the text (p. 732) makes it evident that muscle numbers 2 and 3 are reversed in the ventral view; number 5 in the dorsal view should be number 3; number 6 in the dorsal view should be number 4; and muscle number 4 in the ventral view is apparently intended to represent number 6, but is misdrawn.

THE SYRINX IN OTHER OSCINE GROUPS.

Specimens Examined.

Of approximately 4000 species in about 884 genera contained in the 54 oscine families, I have examined 615 specimens in 533 species and 359 genera. Only two families, the Callaeidae and the Catamblyrhynchidae, are unrepresented in this assemblage. The relative coverage of the various families is shown in Table 5.

Cartilaginous Elements.

A detailed description of the cartilages in each of the oscine genera examined is beyond the scope of this study. With few exceptions, the pattern found in *Corvus* is nearly identical to that of all other genera. As noted by MacGillivray (1839) and by many subsequent authors, the pessulus is lacking in larks (Alaudidae). The only other major structural variant at the family level is the presence of some double B-elements in the swallows (Hirundinidae), except *Pseudochelidon* (Mayr and Amadon, 1951).

Musculature.

In all the oscines examined, the same two pairs of extrinsic and four pairs of intrinsic muscles are present, but there is much variability in the relative positions, size, and attachment of the muscles. Certain families show consistency in syringeal myology and these will be discussed in detail in later papers. I am unable to support the findings of Miskimen (1951) who reported M. bronchialis posticus absent in about 20 of the 29 oscines examined and M. tracheolateralis absent in 10 of the 29. No other author has reported either muscle to be lacking in any oscine. Comparison of my findings with those of Setterwall (1901) and Köditz (1925) leads to the conclusion that the oscine syringeal musculature is far more uniform than is suggested by many recent authors, who base their conclusions on the numbers of muscles described without evaluating the nomenclatorial principles behind the descriptions.

SYRINGEAL DEVELOPMENT

Although the embryology of the syrinx is well understood for some nonpasserine species, such as the domestic duck (*Anas*) and the chicken (*Gallus*), it is virtually unknown for passerines. Wunderlich (1886) provided a brief account of the embryology of the oscine syrinx in the House Sparrow (*Passer domesticus*), but he concerned himself only with the timing of various developmental stages.

The embryos and nestlings described below were dissected primarily to obtain data on posthatching changes in syringeal structure and secondarily to elucidate the developmental homology of syringeal muscles. In each specimen the syrinx was removed from the specimen and examined with a dissecting microscope. The syringes of eight Phoebes (*Sayornis*) and two Cowbirds (*Molothrus*) were sectioned and stained. Four separate staining methods were used (Gurr, 1955): Haematoxylin and Eosin; Foot's modification of the Masson Trichrome stain; Phosphotungstic Acid; and Von Kossa's stain for calcium.

Suborder Tyranni.

Superfamily Furnarioidea.

family furnariidae.

Specimens Examined.

The following three individuals were obtained from the New York Zoological Society. It is uncertain whether they are from the same or separate nests.

Synallaxis cinnamomea Lafresnaye	embryo; NYZS (no number); British Guiana; date unknown; Coll: C.W. Beebe; age (estimated): 1 day prehatching.
Synallaxis cinnamomea Lafresnaye	nestling; NYZS nestling "a"; British Guiana; date unknown; Coll: C.W. Beebe; age (estimated): 1 day posthatching.
Synallaxis cinnamomea Lafresnaye	nestling; NYZS nestling "b"; British Guiana; date unknown; Coll: C.W. Beebe; age (estimated): 2-3 days posthatching.

Cartilaginous Elements.

The three specimens are nearly identical in terms of the configuration of both A- and B-elements and are much like the adult of *Synallaxis cinerascens*. All of the elements are of soft cartilage and are strongly rounded like the B-elements of the adult. The membranes between them are extremely narrow; most of the consecutive elements are in contact. The Processi vocales are present, but the Membranae tracheales are not, all of the A-elements being of uniform width.

Musculature.

The muscles of the embryo and nestlings are exact miniatures of those of the adult *S. cinerascens,* originating and inserting on the same elements as in the latter.

SUPERFAMILY TYRANNOIDEA.

FAMILY COTINGIDAE.

Specimens Examined.

Only the following individual was obtained:

Platypsaris aglaiae (Lafresnaye) nestling, YPM 1532; Mexico, Vera Cruz; 30 Jun 1961; Coll: R.W. Dickerman; age: 12-14 days posthatching.

Cartilaginous Elements.

The cartilaginous elements of the nestling differ from those of the adult only in being rounder in cross-section and proportionately closer together.

Musculature.

The musculature of the nestling is identical to that of the adult in shape and attachments.

FAMILY TYRANNIDAE.

Specimens Examined.

The specimens of *Sayornis* are not listed individually because they vary only in age.

Sayornis phoebe (Latham) 14 embryos, 3 nestlings; U.S.A., Conn.; May 1961; Coll: P. L. Ames; ages: 6 days prehatching to 8 days posthatching.

Fluvicola pica (Boddaert) embryo; NYZS; no data; Coll: C. W. Beebe; age: 1-2 days prehatching.

Fluvicola pica (Boddaert) nestling; NYZS; no data; Coll: C. W. Beebe; age: 1-3 days posthatching.

Fluvicola pica (Boddaert) nestling; NYZS; no data; Coll: C. W. Beebe; age: 4-6 days posthatching.

Pitangus sulphuratus (Linnaeus) nestling; NYZS; British Guiana; date unknown; Coll: C. W. Beebe; age: 8-10 days posthatching.

Cartilaginous Elements.

In *Sayornis* the cartilages begin to form as condensations of the mesenchyme of the respiratory tract late in the sixth or early in the seventh day of the fourteen-day incubation period. I could find no evidence that the formation of an element begins with one particular region or that a complete element is formed through the joining of halves of a divided one. By the eighth day all the cartilages are present, including

the pessulus and the internal cartilages. The latter almost fill the medial surfaces of the short bronchi. At the end of the ninth or the beginning of the tenth day all the elements appear to have attained their ultimate configuration and further development is limited to changes in cross section and in consistency. The B-elements have attained their adult form by the hatching time but the A-elements are still soft and rounded. Staining shows no evidence of calcium deposition, even at two days posthatching. Calcium deposition in the adult syrinx is light and is limited to A-elements.

The specimens of *Fluvicola* and *Pitangus* show the same developmental pattern as comparable specimens of *Sayornis*. The two nestlings of *Fluvicola* are identical to each other, even in minute details. The embryo differs in the pattern of fusion and in lacking an extra component, A-3aR, possessed by the others.

Musculature.

In *Sayornis,* M. tracheolateralis and M. sternotrachealis appear about the beginning of the ninth day. In its earliest recognizable state M. sternotrachealis is attached directly to the trachea, not continuous with M. tracheolateralis as in *Gallus* and many other non-passerines. M. obliquus ventralis appears about a day after the other two muscles. Its fibers appear to develop in the mesenchyme of the ventral surface of the trachea. In 11-day embryos there are only transverse fibers, with no evidence of deep midventral attachment. At 12 or 13 days both of the adult muscle layers are present. At hatching the musculature is identical to that of the adult, but proportionately thinner.

The embryo and nestlings of *Fluvicola pica* are identical to the adult of *F. climazura* except that the muscles are proportionately thinner. The difference in muscle development is particularly evident in *Pitangus,* in which the flatness of the nestling M. obliquus ventralis contrasts with the prominent bulging of the adult muscle.

Suborder Passeres.

Specimens Examined.

I have examined the following 16 embryos and 5 nestlings in 8 genera and 7 families. All of the specimens are in the YPM alcohol collection, but only the nestlings have catalogue numbers. Unless indicated as "measured," ages are estimated by comparison with embryos of known ages. Embryos whose ages are given as "measured" were obtained as freshly laid or slightly incubated eggs and were incubated in a forced-air incubator (37.5°C, 90 percent RH), giving an accuracy of approximately ± 12 hours to age determinations.

FAMILY CORVIDAE.

Corvus corone Linnaeus — nestling; YPM 4482; Aegean, Cyclades Is.; 6 Jun 1959; Coll: G. E. Watson; age: about 10 days posthatching.

FAMILY TROGLODYTIDAE.

Troglodytes troglodytes (Linnaeus) — nestling; YPM 4485; Canada, Quebec; 5 Aug 1949; Coll: S. C. Ball; age: about 10 days posthatching.

Thryothorus griseigularis	embryo; NYZS; British Guiana; 13 Oct 1920; Coll: C. W. Beebe; age: about 1 day prehatching.
FAMILY TURDIDAE.	
Turdus migratorius Linnaeus	2 embryos, 1 nestling; YPM; USA, Conn.; May, 1961; Coll: P.L. Ames; ages: 1 and 3 day prehatching and 2-3 days posthatching.
FAMILY NECTARINIIDAE.	
Cyanomitra dussumieri (Hartlaub)	embryo; YPM; Indian Ocean, Praslin Is.; 23 Jan 1958; Coll: W. D. Hartman; age: 3-4 days prehatching.
FAMILY PLOCEIDAE.	
Passer domesticus (Linnaeus)	3 embryos; YPM; USA, Conn. May, 1961; Coll: P. L. Ames; age: all 2-3 days prehatching, measured.
FAMILY ICTERIDAE.	
Quiscalus quiscala (Linnaeus)	embryo; YPM; USA, Conn.; 24 May 1961; Coll: P. L. Ames; age: about 1 day prehatching.
Molothrus ater (Boddaert)	7 embryos, 2 nestlings; YPM; USA, Conn.; May, 1962; Coll: P. L. Ames; ages: 5-6 days prehatching to 4 days posthatching, measured.
FAMILY FRINGILLIDAE.	
Ammospiza caudacuta (Gmelin)	embryo; YPM; USA, Conn.; 9 Jun 1961; Coll: P. L. Ames; age: 2-3 days prehatching.

Cartilaginous Elements.

The development of syringeal elements was studied most thoroughly in *Molothrus*. The cartilaginous elements are fully present in the youngest embryo, aged approximately eight days. The elements that form the drum are not yet fused. In the course of the next 36 hours elements A-4 through A-7 are fused into the drum, in which joints remain for at least a week after hatching.

All of the other specimens are like the comparable stages of *Molothrus*.

Musculature.

In the eight-day embryo of *Molothrus* I was unable to discern any muscles in the syringeal area. The formation of fibers is rapid; in the later part of the ninth day the syringeal region is surrounded by a nearly continuous sheet of muscle. The Mm.

sternotracheales are visible, but the short intrinsic muscles have not yet formed. By the following day the musculature closely approximates the adult condition, all muscles being clearly visible. By the time of hatching the muscles have the same proportions as in the adult.

In all of the other specimens the development of syringeal musculature closely parallels that of *Molothrus*.

Summary

The timing of the onset of syringeal development in the furnariid *Synallaxis* cannot be determined from available material. At hatching the syrinx is similar to that of the adult but lacks the dorsal and ventral attenuation of elements associated with the Membranae tracheales.

In the Tyrannoidea, if *Sayornis* is typical, the development of syringeal cartilages begins slightly more than halfway through the incubation period. The muscles are first visible about a day later. At the time of hatching the syrinx is identical to that of the adult, except that the A-elements are softer and more rounded, the membranes between elements very narrow, and the muscles less strongly developed. The developmental pattern in *Fluvicola* and *Pitangus* and in the cotinga *Platypsaris* seems to be identical to that of *Sayornis*.

In all of the oscines examined the syringeal cartilages begin their development a little more than halfway through the incubation period; the muscles appear about a day later. At the time of hatching the syrinx is identical to that of the adult, except that the drum is incompletely fused.

MORPHOLOGICAL VARIATION

In order to evaluate a taxonomic character, one must examine the type and degree of variation found at each taxonomic level at which the character is to be applied. For a given taxonomic level, the most important variation is that found in the next lower level. Although the main purpose of this study is to establish relationships among genera and higher categories, an effort has also been made to evaluate intraspecific variation.

INTRASPECIFIC VARIATION.

Intraspecific variation may take the form of geographical, sexual, seasonal, age, or random individual variation. Proper evaluation of each of these requires the examination of series of individuals identical in all other respects, or the examination of a single large series of widely assorted individuals. Such series are not available in alcohol for any suboscine species, but in several species sufficient individuals were examined to allow estimates of the degree of uniformity present. Comparison of even as few as four or five individuals of a species gives an indication of the type and extent of variation present, to the extent that different ages, sexes and geographical regions are represented, although satistical reliability is not to be expected.

Intraspecific variation was studied to a limited degree in the antbird *Formicarius analis* (four specimens) and *Conopophaga lineata* (four specimens), the cotinga *Rhytipterna holerythra* (four specimens), and the tyrannids *Pyrocephalus rubinus* (five specimens) and *Tachuris rubrigastra* (four specimens). In 19 other species three individuals were examined and in 43 species two individuals. In most cases geographical and seasonal data are available, but age and sex are known for very few. Information about syringeal changes with increased age was obtained from the study of embryos and early nestlings. It was not possible to obtain age data on any fully grown specimens, for there is no reliable method of aging suboscines, comparable to the use of skull ossification in oscines.

INTRAGENERIC VARIATION.

Intrageneric variation is usually easier to evaluate than intraspecific, because it is often easy to acquire individuals of many species of some large genera. When single or few individuals of several species are studied, the term "intrageneric" remains more appropriate than "interspecific," for the observed variation represents a combination of intraspecific and interspecific differences.

Inasmuch as the genus is an artificial and highly subjective category, whether a particular type and degree of structural variation is inter- or intrageneric is ultimately

of less importance than its relation to other taxonomic characters, both syringeal and non-syringeal. The differences between *Elaenia flavogaster* and *E. gaimardi* are treated here as intrageneric, following Hellmayr (1927), but they would be intergeneric if one were to separate *E. gaimardi* in the genus *Myiopagis* as is done by many authors. The tyrannid genera *Pipromorpha* and *Mionectes,* although maintained by Hellmayr, were felt by him to be "doubtfully separable," a view shared by Todd (1921). Future authors will probably view the slight differences in syringeal structure as intra- rather than intergeneric.

VARIATION IN CARTILAGINOUS ELEMENTS.

Fusion of A-elements.

The degree of totality of fusion and the precise regions of fusion are variable within rather narrow limits at the intraspecific level. Up to the age of about a year, and possibly more in some groups, the degree of fusion may be correlated with age. Little variation in fusion was found in oscines after the first few months of age. The slow development of the Membranae tracheales in the furnariid *Synallaxis* suggests that fusion is delayed in members of the Furnarioidea. In some species in the Tyrannidae (*Leptotriccus sylveolus, Myiozetetes similis, M. cayanensis* and *Tolmomyias sulphurescens,* for example) individuals differ in that elements wholly or partially fused in one may be devoid of fusion in another. In the large majority of species in which two or more specimens were examined the general pattern of fusion was the same for all individuals of the species, the variation being limited to the number of fused elements and the degree of totality. In suboscine species whose syringes have many fused elements (the woodcreeper *Glyphorhynchus spirurus,* the manakin *Chiroxiphia caudata,* and various species of the flycatcher genus *Elaenia*) considerable fusion is present in all individuals, but the exact number of elements involved is often variable. In one of my two specimens of *Glyphorhynchus spirurus* the drum is of seven elements; in the other it is of four elements. In *Elaenia chiriquensis* one of the three individuals examined has a drum of three elements; in the other two it is of four elements. In all three the fusion is complete and the pessulus is fused to the posterior element of the drum (A-3).

The degree of fusion of elements may vary less within some genera than within certain species of other genera. Among the suboscines examined only *Tyrannus, Myiarchus, Myiozetetes* and *Elaenia* were available in sufficient numbers to allow even tentative estimates of both intrageneric and intraspecific variation and only in the last two genera was there significant fusion. In both *Myiozetetes similis* and *M. cayanensis* intraspecific variation equaled that found in the genus; individuals with no fusion and those with three fused elements were found in each species.

In *Elaenia* the degree of variation in the genus exceeded the slight amount (one element among the three specimens of *E. chiriquensis*) found in either of the two species represented by multiple specimens. There was, however, less variation in the amount of fusion among the 12 specimens of nine species in *Elaenia* than between the two individuals of *Leptotriccus sylveolus* studied. Apparently the functional significance of fusion is different in the two genera.

There appears to be little or no intraspecific or intrageneric variation in fusion of B-elements. This type of fusion was found only in *Tyrannus* and a few similar genera and in *Tyranniscus chrysops.*

In the oscines, the only observed fusion was that of the lower A-elements that comprise the drum. The composition of the drum appears to be uniform at least up to the generic level. The configuration of the drum was noted in only a few of the many oscines studied, as it was desirable to retain the muscles for future study.

Configuration of Individual Elements.

The number of divided, double or incomplete elements present is often subject to intraspecific variation. The type and extent of variation of a given element depends strongly on the configuration of adjacent elements. In the tyrannid *Colopteryx,* in which there is a long series of dorsally incomplete elements (A-5 through A-12 in my specimen), A-8 may be considered to be uniform. Since the length of the series of incomplete elements is variable—in Müller's specimen it extended through A-16—the configuration of A-13 or A-14 is undoubtedly variable. The variation present is really in the length of the dorsal "slot" complex, expressed in the configuration of the individual element. In *Empidonax minimus* A-5 is complete in two of the three specimens and incomplete dorsally in the third, A-4 being divided and A-6 complete in all three. Similar variation occurs in the Furnarioidea. As well as variation in the configuration of elements, there are differences in the degree of attenuation of elements at the anterior edges of the Membranae tracheales.

In short, the most variable region in the suboscines is the point of change from the divided A-elements at the posterior end of the syrinx (A-1 invariably being divided) to the complete anterior elements. An element is more likely to vary between divided and incomplete than between divided and complete and none was found to vary between dorsally and ventrally incomplete. There is a continuum from divided through incomplete to complete. The double condition may be considered to lie on the opposite side of divided from the "incompletes," there being no case of an element varying between double and incomplete. Double and divided configurations for the same element are found within a species (*Pyrocephalus rubinus*) or a genus (*Myiarchus*). In one specimen of *Pyrocephalus* A-4 is intermediate between divided and double, extending partway across the internal tympaniform membrane from the dorsal edge.

The configuration of cartilaginous elements in oscines appears to be uniform, even in small details, among individuals of a species and species of a genus. This is consistent with general homogeneity of the syrinx among the oscines.

Shape of Elements.

In general the proportions and contours of a given element are variable in suboscines, even at the intraspecific level. Variation is not extreme, however, being limited to the degree of spatulation, of rounding, or of other modifications. The contours of a given element appear to be influenced by the shapes and, particularly, the positions of adjacent elements. If the ends of an incomplete element meet in line with each other, they are likely to be squared off (e.g. *Tyrannnus,* Pl. 10); if they

are not aligned, but each end lies opposite a space, they are more apt to be pointed (see *Legatus,* Pl. 7). The latter case is of common occurrence when strong asymmetry is present.

There is little variation in the shapes of elements that bear muscle insertions. A-1 and B-1 are relatively uniform up to the generic level. Other elements may also exhibit great uniformity. In the large cotinga, *Pyroderus,* the sculptured edges of the lower A-elements are virtually identical in my two specimens and that examined by Garrod (1878).

In the pittas and some broadbills, the lower A-elements have irregular edges and frequent holes (membranous, of course). I have not examined more than one specimen in any species of the genus *Pitta,* but at the intrageneric level these irregularities appear to be randomly distributed.

Asymmetry.

Various degrees of bilateral asymmetry are found in many suboscine syringes. The most common and most variable type of asymmetry involves the width or shape of an element. The opening of a divided or dorsally incomplete element is frequently displaced from the midline, usually to the left. Displacement at the ventral midline is rare.

Asymmetrical fusion is of frequent occurrence in the superfamily Tyrannoidea, but appears to be individually variable. Twenty-one individuals of 20 genera were found to possess unequal fusion. In most cases the fusion is partial, often involving only the ends of two elements. Often the pessulus is involved. In the flycatcher *Myiophobus,* (Pl. 20) the pessulus in the only specimen examined is fused dorsally to A-4 on the right and to A-5 on the left. In many other examples the pessulus is fused only to one side of one element. Of the 20 genera in which unequal fusion was found, two or more specimens were examined in 13. Two of seven individuals of *Myiozetetes* were asymmetrical in this respect, but in several other tyrannid genera of which seven or more specimens were examined (*Tyrannus, Myiarchus, Elaenia*) no asymmetry was found. In other respects the cartilaginous structure of *Myiozetetes* shows much more variation than the other genera. It thus appears that the tendency toward asymmetry, as well as other types of variation, is greater in some genera than in others.

Less asymmetrical fusion was found in the superfamily Furnarioidea than in the Tyrannoidea. What asymmetry there is appears limited to the elements posterior to the Membranae tracheales (e.g. *Taraba,* Pl. 3).

The most extreme form of asymmetry found in the suboscine syrinx is the presence of an "extra" component on one side. Extra components were found in 17 individuals of 11 genera in the Tyrannoidea. None were found in any genus of the Furnarioidea or of the suborders Eurylaimi, Menurae, or Passeres. It is noteworthy that in every case the extra component is on the right side. This uniformity suggests a functional significance of the extra element, perhaps correlated with the slight but regular bend of the trachea to the left in the region of the syrinx. The distribution of extra components appears to be less individually variable than other forms of asymmetry. Both specimens of *Onychorhynchus* and of *Habrura,* all three specimens of *Microtriccus,* and three out of four specimens of *Pitta* have extra components. Long series of several

of these genera should be examined to evaluate fully the degree of variation in this form of asymmetry.

Pessulus.

The degree of variation in the pessulus is itself highly variable, correlated with the overall variation in the structure of the syrinx. All members of the suboscine superfamily Furnarioidea and all of the oscine family Alaudidae (larks) lack the pessulus entirely. In the superfamily Tyrannoidea specimens of 24 genera in four families were found lacking the pessulus. In most of the tyrannoid cases the anterior ends of the internal tympaniform membranes, which are usually attached to the pessulus, are attached to some other form of cartilage, the shape of which varies greatly. Such cartilages are also found in many syringes possessing pessuli.

In 21 genera of the Tyrannidae specimens were found lacking the pessulus. In three of these genera (*Tyrannus, Myiobius* and *Empidonax*) individuals both with and without pessuli were found, and the number of such genera might well be higher if large series of some other genera were examined. Of three specimens of *Tyrannus tyrannus* from the same locality in Connecticut, two have the pessulus, one does not.

Despite the variability of the pessulus down to the level of populations, the range of variation within a species or a genus is limited. When the pessulus is entirely lacking in some individuals (or species), it is present only in form of a short bar or one incompletely fused in the remainder of the species (or genus). In no genus were individuals without pessuli and those with completely fused pessuli found.

Cartilaginous Plug or Sheet.

There is little intraspecific or intrageneric variation in the presence or absence of a dorsomedial plug or sheet. The contours of this cartilage seldom show differences among members of a well-defined genus.

Other areas of soft cartilage joining A-elements, such as are present in the tyrannid *Tachuris* and the antbird *Formicarius,* were found to be highly uniform within the small series of specimens examined.

Internal Cartilages.

Found only in tyrant flycatchers, some cotingas, the sharpbill (*Oxyruncus*), and one genus each of manakin (*Schiffornis*), asity (*Neodrepanis*), and New Zealand wren (*Acanthisitta*), internal cartilages are among the most uniform of cartilaginous components at the intrageneric level. Members of a species have similar but not always identical internal cartilages. Both J- and J-shaped cartilages are found in the same species and the proportions of bars and triangles vary intraspecifically, but rounded triangles were not found in the same species or even in the same genus as J-shaped cartilages. The more intricate shapes, such as those in *Corythopis, Leptopogon, Platyrinchus,* and *Pipromorpha,* are subject to even less variation than the simpler ones.

The number of pairs of internal cartilages was also uniform, being one in most genera. Of the genera possessing two pairs, only *Myiarchus* was studied in sufficient depth to allow an estimate of the degree of variation to be expected. In all seven individuals of five species there were two pairs of internal cartilages present and these were uniform in shape and position.

The only genus examined with variation in the number of internal cartilages is *Tolmomyias*. The two species examined differ so much that only the study of a larger series of specimens will permit evaluation of the variation present.

MUSCULATURE.

M. Tracheolateralis.

In this study I have concerned myself only with the position, width and insertion of this muscle. The position and width are extremely uniform up to the generic level, the only exception being the tyrannid genus *Tolmomyias*, which is also variable in other aspects of the syrinx. In suboscines the degree of variation of the insertion of M. tracheolateralis is correlated with the presence of intrinsic muscles. When none are present, as in the Eurylaimidae, some of the Furnarioidea, and many of the Tyrannoidea, it inserts near the A-B junction, the mode and place of insertion being intragenerically uniform. An exception is the broadbill genus *Smithornis*, in which the insertion is higher on the trachea and the precise element of insertion apparently variable.

In the presence of intrinsic musculature the exact region of insertion of M. tracheolateralis is more variable than when no intrinsic muscles are present, but the variation is not extreme. When the insertion is immediately anterior to the origin of the intrinsic muscles, as in many tyrannid flycatchers, there is seldom more than one or two elements' variation in its position.

The degree of variation is related to other features of the syrinx. When a well-developed drum is present, M. tracheolateralis usually inserts on its anterior edge, but the number of elements comprising the drum may be variable (see above). Where it interacts with the intrinsic muscles, M. tracheolateralis shows considerable uniformity. It was found to be constant in several species of *Empidonax* and *Myiochanes*, in which it extends beneath the intrinsic muscle to insert on A-2, and in *Leptopogon* and *Pyrocephalus*, in which it extends posteriad between the ventral intrinsic muscles.

M. Sternotrachealis.

The mode of insertion of this muscle appears to be uniform well above the generic level in the superfamily Furnarioidea and the suborder Passeres. Considerably more variation is found in the Tyrannoidea.

In most genera of the Tyrannidae the type of insertion of M. sternotrachealis is related to the relative cross-sectional area of the muscle, which is approximately uniform within most of the genera studied. A thick muscle usually inserts by two or three fasciculi, each with a different type of insertion. In some individuals of a genus

(or on one side of an individual only) a fasciculus may be entirely missing. The proportions of the various fasciculi may vary greatly within a species, as may the anteroposterior position of the insertion. The most variable form of insertion, in terms of presence or absence, is that of continuity with M. tracheolateralis, but when only this form of insertion is present it is more uniform.

The anteroposterior position and the area covered by the insertion appear to vary most when all or nearly all of the muscle inserts directly. In *Myiarchus,* for example, the most posterior element of insertion varies from A-11 to A-15. In this case the variation appears to be interspecific, but similar variation in *Myiozetetes* seems to be intraspecific. The samples on hand are too small for positive determination of the basis of variation.

In summary, M. sternotrachealis displays a rather uniform appearance within a genus of tyrant flycatchers. This uniformity is reflected in the general proportions of the muscle and in the type of insertion. In the anteroposterior position of its insertion the muscle is quite variable.

In other families of the Tyrannoidea few individuals of most genera were examined. In the becards of the genus *Pachyramphus* the situation is like that of the Tyrannidae. In the Furnarioidea there is less variation at the intrageneric level, but the exact position of the insertion is often variable. In *Conopophaga* whether the muscle inserts partly on the Processus vocalis or wholly on the trachea is intraspecifically variable. The position of the insertion of M. sternotrachealis is much more uniform in the oscines, up to the family level.

Intrinsic Muscles.

There are several sources of potential variation in the intrinsic musculature, principally the mode and position of the origin and insertion and the general shape of the muscle.

In the superfamily Tyrannoidea intrinsic muscles are found only in a few cotingas and manakins, the sharpbill, and most of the tyrant flycatchers. In all cases in which more than one member of a species was examined the mode and position of origin was found to be intraspecifically uniform. With very few exceptions, the uniformity extends to the generic level. In some of the exceptions (*Pitangus, Tolmomyias, Tyranniscus*) the variation in intrinsic muscles was accompanied by interspecific differences in other features of the syrinx. In other genera the variation, although clearly visible, was restricted to a particular aspect of the musculature. In *Pyrocephalus rubinus* there is an unusually large amount of individual variation in the width of the intrinsic muscle, M. obliquus ventralis. In *Sayornis* there is intrageneric variation in the presence of transverse continuity of the superficial muscle layer. In *Elaenia* there is variation, apparently interspecific, in the mode of origin of M. obliquus ventralis. In the last genus there is some intrageneric variation in the degree of separation of the lateral muscle from the ventral one.

The mode of insertion of an intrinsic muscle is more subject to intrageneric variation than the mode of origin, but most of the differences are quantitative. In *Suiriri* and *Phaeomyias* the width of the tendon of M. obliquus ventralis is variable, while in *Elaenia* the mode of insertion, tendinous or direct, and the element of insertion are

variable. In most of the genera of tyrant flycatchers in which individuals of several species were examined (*Xolmis, Tyrannus, Myiarchus, Empidonax*) the shape and attachment of the intrinsic muscles were found to be highly uniform at the generic level.

In the Furnarioidea and the Passeres the intrinsic muscles are more uniform than in the Tyrannoidea. In the Formicariidae and Furnariidae there is intrageneric variation in muscle origins, comparable to that found in the Tyrannidae, i.e. positional differences of one or two elements, without differences in the interrelationships of the various muscles. Not even this much variation has been found in any genus of the suborder Passeres.

MORPHOLOGICAL SUMMARY

The major structural features of the syringes examined in this study are summarized in the following compilations. The first outline summarizes the distribution of individual syringeal features. Because of fundamental and consistent differences between the "tracheophone" type of syrinx, with Membranae tracheales and associated structures, and the type found in the rest of the passerines, I have divided the detailed compilation into two categories, those with and those without Membranae tracheales. Within each category the structural variations are differentiated in as much detail as is feasible. In some features of the syrinx, such as the degree of fusion of elements or the positions of muscle origins, the number of variations is so great and the differences between adjacent members of the morphological series so slight that grouping into many small categories would create an artificial and unreal order. To minimize this artificiality, I have avoided a detailed summary of features with many subtle variations and have established instead broad categories which indicate the relative degrees to which a feature is present. The positions of muscles relative to the planes of symmetry of the syrinx are more uniform and the morphological variations more easily classified. Within each morphological division, taxonomic groups are listed in the conventional order, as in earlier sections.

When specimens of a taxonomic group fall into more than one division of a structural feature the taxonomic name is followed by "(part)" and placed in each appropriate section. Inasmuch as most genera are represented in this study by only single specimens, predictably few are listed under more than one heading. The variation found in a given structural feature is best understood by observing the distribution of genera, such as *Tyrannus, Myiarchus* and *Elaenia*, in which several individuals and species were examined.

DETAILED SUMMARY OF MORPHOLOGY.

Category I. Lower trachea dorsoventrally compressed; elements in compressed region attenuated and sometimes absent, forming dorsal and ventral "windows" or Membranae tracheales; lateral cartilaginous or bony rods or plates (Processi vocales) present; pessulus absent.

Suborder Tyranni (part) : Superfamily Furnarioidea

A. Cartilaginous elements.

1. Fusion of elements.
   a. No fusion.
      Furnariidae (part) : *Asthenes, Automolus, Geositta, Sclerurus.*

Rhinocryptidae (part) : all except *Melanopareia.*
Formicariidae.

b. Two or more elements fused, forming a "drum".
Dendrocolaptidae.
Furnariidae (part) : all except those in (a), above.
Rhinocryptidae (part) : *Melanopareia.*

2. Processi vocales.

a. Very small; attached to surrounding elements by fibrous connective tissue.
Formicariidae (part) : all except *Formicarius, Chamaeza, Grallaria,* and *Conopophaga.*

b. Prominent straight bars, thicker than those in (a), rather uniform in width.
Formicariidae (part) : *Formicarius, Chamaeza, Grallaria, Gonopophaga.*
Rhinocryptidae (part) : *Teledromas.*

c. Wide base; narrow "stalk"; flat, flared anterior end.
Furnariidae (part) : all except *Geositta.*
Rhinocryptidae (part) : all except *Teledromas.*

d. Wide base; broad central part; prominent dorsal and ventral horns.
Dendrocolaptidae.
Furnariidae (part) : *Geositta.*

B. Musculature.

1. Extrinsic muscles (two pairs present in all passerines).

a. M. tracheolateralis.

i. Width (approximate average along the 12 elements immediately anterior to the Membranae tracheales).

a) Narrow (each of the pair less than 30° of tracheal circumference in width).
Formicariidae (part) : *Formicarius, Grallaria, Conopophaga.*
Rhinocryptidae (part) : *Teledromas.*

b) Medium (30-60° of tracheal circumference).
Dendrocolaptidae.
Rhinocryptidae (part) : all except *Teledromas.*

c) Broad (more than 60° of tracheal circumference).
Furnariidae.
Formicariidae (part) : all except *Formicarius, Grallaria* and *Conopophaga.*

ii. Insertion.

a) On the drum and/or other elements immediately anterior to the Membranae tracheales.
Dendrocolaptidae.
Furnariidae.
Formicariidae (part) : *Cymbilaemus, Sakesphorus, Thamnophilus, Dysithamnus, Thamnomanes, Herpsilochmas, Neorhopias, Cercomacra, Pyriglena, Myrmoborus, Hypocnemis, Myrmeciza, Gymnopithys, Hylophylax.*
Rhinocryptidae (part) : *Pteroptochos, Rhinocrypta, Triptorhinus.*

b) On the anterior end of the Processus vocalis.
Formicariidae (part) : *Formicarius, Grallaria, Conopophaga* (part).
Rhinocryptidae (part) : *Scelorchilus, Teledromas, Melanopareia.*

c) On the drum and/or elements anterior to the Membranae tracheales *and* on the anterior end of the Processus vocalis.
Formicariidae (part) : *Taraba, Pygiptila, Chamaeza, Conopophaga* (part).
Rhinocryptidae (part) : *Scytalopus.*

d) On elements anterior to the Membranae tracheales and (superficial fibers) in continuity with M. sternotrachealis.
Formicariidae (part) : *Myrmotherula, Myrmorchilus.*

b. M. sternotrachealis.

i. Type and region of insertion.

a) Directly on the anterior end of the Processus vocalis.
Dendrocolaptidae.
Furnariidae.
Formicariidae (part) : *Formicarius, Chamaeza, Grallaria.*
Rhinocryptidae.

b) In part on the anterior end of the Processus and in part on the lateral surface of elements immediately anterior to the Membranae.
Formicariidae (part) : *Conopophaga* (part).

c) On the lateral surfaces of several elements immediately anterior to the Membranae.
Formicariidae (part) : *Conopophaga* (part).

d) By two fasciculi; one to the anterior end of the Processus; the other to the dorsolateral surfaces of the elements immediately anterior to the Membranae, inserting adjacent to the dorsal edge of M. tracheolateralis, or partially in continuity with that muscle.
Formicariidae (part) : all except *Formicarius, Chamaeza, Grallaria* and *Conopophaga.* (Fiber continuity only in *Myrmotherula* and *Myrmeciza.*)

2. Intrinsic muscles.

a. Number present.

i. None.
Formicariidae (part) : *Formicarius, Chamaeza, Grallaria, Conopophaga.*
Rhinocryptidae (part) : *Teledromas.*

ii. One pair.
Formicariidae (part) : all except *Formicarius, Chamaeza, Grallaria* and *Conopophaga.*
Rhinocryptidae (part) : all except *Teledromas.*

iii. Two pairs.
Dendrocolaptidae.
Furnariidae.

b. Position of muscle origin.

i. When one pair present.

a) On the ventral and ventrilateral surfaces of several elements immediately anterior to the Membranae tracheales.
Formicariidae (part) : all possessing intrinsic muscles.

b) On the lateral and/or dorsolateral surfaces of several elements immediately anterior to the Membranae tracheales.
Rhinocryptidae (part) : all possessing intrinsic muscles.

ii. When two pairs present.

a) Dorsal pair originates on the lateral and dorsolateral surfaces of the several elements anterior to the Membranae tracheales (on the anterior edge of the drum, when one is present) ; ventral pair originates on the lateral and ventrilateral surfaces of the same elements.
Dendrocolaptidae.
Furnariidae.

c. Position of muscle insertion.

i. When one pair present.

a) On the anterior end of the Processus, dorsally and anteriorly adjacent to the insertion of M. sternotrachealis.
Formicariidae (part) : all possessing intrinsic muscles.

b) On the anterior end of the Processus, ventrally adjacent to the insertion of M. sternotrachealis.
Rhinocryptidae (part) : all except *Teledromas* and *Melanopareia.*

c) Along nearly the entire length of the Processus.
Rhinocryptidae (part) : *Melanopareia.*

ii. When two pairs present.

a) Dorsal pair inserts on the anterior end of the Processus, posterodorsal to the insertion of M. sternotrachealis; ventral pair inserts on the anterior end of the Processus, posteroventral to the insertion of M. sternotrachealis.
Furnariidae (part) : all except *Geositta.*

b) On the dorsal and ventral horns, respectively, of the Processus.
Dendrocolaptidae.
Furnariidae (part) : *Geositta.*

CATEGORY II. Lower trachea cylindrical or nearly so. Membranae tracheales and Processi vocales absent.

Suborder Eurylaimi
Suborder Tyranni (part) : Superfamily Tyrannoidea
Suborder Menurae
Suborder Passeres

A. Cartilaginous elements.

1. Fusion of A-elements.

a. No fusion.

i. Membranous areas between elements.
Eurylaimidae (part) : *Smithornis, Cymbirhynchus, Eurylaimus.*
Cotingidae (part) : *Heliochera, Casiornis, Pheonicircus, Attila, Rhytipterna, Platypsaris, Pachyramphus, Iodopleura, Conioptilon.*
Pipridae (part) : *Piprites, Corapipo, Schiffornis, Ilicura.*

Tyrannidae (part): *Xolmis, Phaeotriccus, Knipolegus, Neoxolmis, Ochthoeca, Sayornis, Colonia, Gubernetes, Yetapa, Agriornis, Muscisaxicola, Lessonia, Entotriccus, Lichenops, Muscipipra, Fluvicola, Arundinicola, Pyrocephalus, Muscigralla, Satrapa, Machetornis, Myiozetetes* (part), *Mitrephanes, Myiophobus, Terenotriccus, Onychorhynchus, Aphanotriccus, Platyrinchus, Myiornis, Lophotriccus, Euscarthmornis, Colopteryx, Hemitriccus, Oncostoma, Leptotriccus* (part), *Todirostrum* (part), *Tachuris, Phyllomyias, Leptopogon.*

Oxyruncidae.

Phytotomidae.

Pittidae.

Philepittidae.

ii. Closely fitted or overlapping elements.

Eurylaimidae (part): *Psarisomus, Serilophus, Calyptomena.*

Cotingidae (part): *Cotinga, Xipholena, Euchlornis, Carpodectes, Tityra* (part), *Querula, Cephalopterus, Perissocephalus, Gymnoderus.*

Tyrannidae (part): *Pitangus, Empidonax, Blacicus.*

b. Partial fusion (less than the full length of any element).

i. Ventral and/or dorsal midline only.

Cotingidae (part): *Pyroderus, Laniocera.*

Tyrannidae (part): *Capsiempis, Colorhamphus.*

ii. More than midline, but not complete fusion.

Cotingidae (part): *Tityra* (part).

Tyrannidae (part): *Tyrannus, Muscivora, Myiodynastes, Tolmarchus, Megarhynchus, Conopias, Tyrannopsis, Legatus, Myiarchus, Eribates, Nesotriccus, Pyrrhomyias, Myiobius, Nuttallornis, Tolmomyias, Habrura, Phylloscartes, Leptotriccus* (part), *Todirostrum* (part), *Serpophaga, Corythopis, Spizitornis, Mecocerculus, Inezia, Stigmatura, Tyrannulus, Tyranniscus.*

c. Complete (full length) fusion of two or more elements.

i. Involving divided or double elements only.

Cotingidae (part): *Procnias.*

Pipridae (part): *Manacus.*

Tyrannidae (part): *Phaeomyias* (part).

ii. Involving complete elements, with or without other types of elements.

Cotingidae (part): *Rupicola.*

Pipridae (part): *Pipra, Chiroxiphia.*

Tyrannidae (part): *Empidonomus, Sirystes, Myiozetetes* (part), *Myiarchus* (part), *Cnemotriccus, Pseudocolopteryx, Euscarthmus, Elaenia, Suiriri, Phaeomyias* (part), *Microtriccus, Leptopogon, Pipromorpha, Mionectes.*

2. Fusion of B-elements.

a. B-1 and B-2 joined by a short bridge.

Tyrannidae (part): *Tyrannus, Muscivora, Empidonomus, Myiodynastes, Megarhynchus, Conopias, Tyrannopsis, Tolmarchus, Tyranniscus.*

b. B-3 and B-4 joined by a short bridge.

Tyrannidae (part): *Pitangus* (part).

3. Pessulus.
   a. Absent.
      Cotingidae (part) : *Tityra* (part).
      Pipridae (part) : *Chiroxiphia.*
      Tyrannidae (part) : *Xolmis, Knipolegus, Neoxolmis, Satrapa, Entotriccus, Lessonia, Tyrannus* (part), *Megarhynchus, Pitangus, Sirystes, Myiarchus, Myiobius* (part), *Nuttallornis, Empidonax* (part), *Aechmolophus, Platyrinchus, Phylloscartes, Serpophaga, Spizitornis, Mecocerculus, Inezia, Tachuris.*
      Pittidae (part).
      Suborder Passeres (part) : Alaudidae.
   b. Partial pessulus.
      Tyrannidae (part) : *Tyrannus* (part), *Legatus, Myiodynastes, Myiozetetes* (part), *Tolmarchus, Blacicus, Phyllomyias, Pittidae* (part).
   c. Full pessulus, but not wholly fused to other components.
      Cotingidae (part) : *Cotinga, Pyroderus, Procnias, Attila, Phoenicircus, Casiornis, Rhytipterna, Iodopleura, Laniocera, Pachyramphus* (part).
      Pipridae (part) : *Pipra, Manacus, Ilicura.*
      Tyrannidae (part) : *Arundinicola, Sayornis, Machetornis, Myiozetetes* (part), *Myiophobus, Terenotriccus, Onychorhynchus, Myiobius* (part), *Empidonax* (part), *Myiochanes, Tolmomyias, Rhynchocyclus, Oncostoma, Euscarthmornis, Lophotriccus, Colopteryx, Myiornis, Hemitriccus, Habrura, Capsiempis, Pseudocolopteryx, Todirostrum* (part), *Stigmatura, Microtriccus, Leptopogon.*
      Oxyruncidae.
      Acanthisittidae.
   d. Full pessulus, fused to other components at both ends.
      Eurylaimidae.
      Cotingidae (part) : *Xipholena, Euchlornis, Lipaugus, Heliochera, Pachyramphus* (part), *Platypsaris, Tityra* (part), *Querula, Carpodectes, Cephalopterus, Perissocephalus, Gymnoderus, Conioptilon, Rupicola.*
      Pipridae (part) : *Piprites, Corapipo, Schiffornis.*
      Tyrannidae (part) : *Phaeotriccus, Pyrocephalus, Conopias, Mitrephanes, Pyrrhomyias, Cnemotriccus, Pogonotriccus, Todirostrum* (part), *Nesotriccus, Euscarthmus, Corythopis, Colorhamphus, Suiriri, Elaenia, Phaeomyias, Tyranniscus, Pipromorpha, Mionectes.*
      Phytotomidae.
      Philepittidae.
      Suborder Menurae.
      Suborder Passeres (part) : all except Alaudidae.

4. Cartilaginous plug or sheet, present only in the following:
   Cotingidae (part) : *Tityra.*
   Pipridae (part) : *Piprites.*
   Tyrannidae (part) : *Xolmis, Phaeotriccus, Pyrocephalus, Knipolegus, Neoxolmis, Gubernetes, Agriornis, Muscisaxicola, Satrapa, Entotriccus, Muscipipra, Yetapa, Colonia, Ochthoeca, Sayornis, Lichenops, Muscigralla, Megarhynchus, Legatus, Sirystes, Myiarchus, Eribates, Nuttallornis, Aphanotriccus, Empidonax, Blacicus, Mitrephanes, Stigmatura.*

5. Internal cartilages.
   a. Absent.
      Cotingidae (part): all except *Attila, Casiornis, Rhytipterna, Laniocera, Pachyramphus, Platypsaris* and *Iodopleura.*
      Pipridae (part): all except *Schiffornis.*
      Tyrannidae (part): *Colopteryx, Euscarthmornis, Hemitriccus, Oncostoma.*
      Phytotomidae.
      Pittidae.
      Philepittidae (part): *Philepitta.*
      Acanthisittidae (part): *Xenicus.*
      Suborder Menurae.
      Suborder Passeres.
   b. Present.
      i. Triangular.
         Cotingidae (part): *Iodopleura.*
         Tyrannidae (part): *Xolmis, Phaeotriccus, Knipolegus, Lichenops, Colonia, Sayornis* (part), *Nuttallornis, Aphanotriccus, Blacicus, Mitrephanes, Cnemotriccus, Tolmomyias* (part), *Colorhamphus.*
         Philepittidae (part): *Neodrepanis.*
      ii. Straight bars.
         Cotingidae (part): *Pachyramphus, Platypsaris.*
         Tyrannidae (Part): *Agriornis, Sayornis* (part), *Muscigralla, Arundinicola, Tyrannus, Myiodynastes, Pitangus* (part), *Myiozetetes, Nesotriccus, Myiochanes, Aechmolophus, Myiobius, Pyrrhomyias, Myiophobus, Tolmomyias* (part), *Myiornis, Habrura, Capsiempis, Pseudocolopteryx, Pogonotriccus, Phylloscartes, Euscarthmus, Serpophaga, Spizitornis, Mecocerculus, Inezia, Stigmatura, Phaeomyias, Tyrannulus, Phyllomyias, Tyranniscus, Leptopogon.*
         Acanthisittidae (part): *Acanthisitta.*
      iii. J- or ⅃-shaped.
         Cotingidae (part): *Attila, Casiornis, Rhytipterna.*
         Pipridae (part): *Schiffornis.*
         Tyrannidae (part): *Pyrocephalus, Gubernetes, Satrapa, Entotriccus, Muscivora, Megarhynchus, Conopias, Pitangus* (part), *Legatus, Sirystes, Empidonax, Myiarchus, Eribates, Terenotriccus.*
      iv. Other shapes.
         Tyrannidae (part):
            Lessonia, shield-shaped.
            Machetornis, elliptical.
            Onychorhynchus, peanut-shaped, with fat capsules.
            Platyrinchus, straight bars with ⅃-shaped extensions.
            Rhynchocyclus, S-shaped.
            Leptotriccus, flattened spheres, each with one long stem.
            Corythopis, flattened spheres, each with two long stems.
            Todirostrum, straight sheets, fused to A-1 through A-5.
            Tachuris, circular plates, with fat capsules.
            Elaenia, Microtriccus, Camptostoma, straight or slightly curved bars, with semicircular ventrad extensions.

Pipromorpha, Mionectes, long, slightly curved blades, extending posteriad from flattened hemispheres, the whole connected to an A-element by a short stem.

Oxyruncidae: Long narrow, slightly curved bars.

v. Second (ventral) pair present.

Cotingidae (part) : *Attila, Casiornis, Rhytipterna, Laniocera.*

Tyrannidae (part) : *Agriornis, Arundinicola, Myiarchus, Tolmomyias* (part), *Rhynchocyclus, Todirostrum, Inezia, Tyrannulus.*

B. Musculature.

1. Extrinsic muscles: two pairs present in all passerines.

a. M. tracheolateralis.

i. Width (approximate average width along the 12 elements immediately anterior to insertion).

a) Narrow (each muscle less than 30° of tracheal circumference).

Eurylaimidae.

Cotingidae (part) : *Phoenicircus, Heliochera, Cotinga, Xipholena, Tityra, Querula, Pyroderus, Cephalopterus, Perissocephalus, Conioptilon, Rupicola.*

Pipridae (part) : *Piprites.*

Tyrannidae (part) : *Ochthoeca, Myiodynastes, Pitangus, Legatus, Sirystes, Nesotriccus, Terenotriccus, Myiobius, Onychorhynchus, Rhynchocyclus, Tolmomyias, Todirostrum.*

Phytotomidae.

Pittidae.

Acanthisittidae.

b) Medium (30-60° of tracheal circumference).

Cotingidae (part) : *Euchlornis, Lipaugus, Pachyramphus, Platypsaris.*

Pipridae (part) : *Schiffornis.*

Tyrannidae (part) : *Conopias, Myiozetetes, Pyrrhomyias, Oncostoma, Lophotriccus, Euscarthmornis, Colopteryx, Myiornis, Hemitriccus, Pogonotriccus, Stigmatura, Corythopis, Inezia, Colorhamphus, Leptopogon, Pipromorpha, Mionectes.*

Oxyruncidae.

c) Broad (more than 60° of tracheal circumference).

Cotingidae (part) : *Attila, Laniocera, Rhytipterna, Gymnoderus, Casiornis, Iodopleura.*

Pipridae (part) : *Pipra, Chiroxiphia, Corapipo, Manacus, Ilicura.*

Tyrannidae (part) : *Agriornis, Xolmis, Muscisaxicola, Lessonia, Neoxolmis, Sayornis, Colonia, Gubernetes, Yetapa, Knipolegus, Phaeotriccus, Entotriccus, Lichenops, Muscipipra, Fluvicola, Arundinicola, Pyrocephalus, Muscigralla, Machetornis, Muscivora, Tyrannus, Empidonomus, Megarhynchus, Tyrannopsis, Tolmarchus, Myiarchus, Eribates, Nuttallornis, Myiochanes, Blacicus, Empidonax, Aechmolophus, Cnemotriccus, Mitrephanes, Aphanotriccus, Myiophobus, Platyrinchus, Tolmomyias* (part), *Leptotriccus, Phylloscartes, Capsiempis, Euscarthmus,*

Pseudocolopteryx, Habrura, Tachuris, Spizitornis, Serpophaga, Mecocerculus, Elaenia, Suiriri, Phaeomyias, Camptostoma, Phyllomyias, Tyranniscus, Tyrannulus, Microtriccus, Sublegatus.
Philepittidae.
Suborder Menurae.
Suborder Passeres.

ii. Position.

a) Members of the pair do not touch at the ventral midline.
Eurylaimidae.
Cotingidae (part): *Phoenicircus, Heliochera, Cotinga, Xipholena, Carpodectes, Euchlornis, Lipaugus, Tityra, Querula, Pyroderus, Cephalopterus, Perissocephalus, Gymnoderus, Conioptilon, Procnias, Rupicola.*
Pipridae (part): *Piprites, Schiffornis.*
Tyrannidae (part): *Legatus, Sirystes, Myiodynastes, Conopias, Myiozetetes, Pitangus, Myiarchus, Eribates, Nesotriccus, Terenotriccus, Aphanotriccus, Myiobius, Onychorhynchus, Tolmomyias* (part), *Rhynchocyclus, Todirostrum, Oncostoma, Euscarthmornis, Lophotriccus, Colopteryx, Myiornis, Hemitriccus, Spizitornis, Elaenia* (part), *Suiriri, Sublegatus, Phaeomyias, Tyrannulus.*
Phytotomidae.
Pittidae.
Philepittidae.
Acanthisittidae.
Suborder Menurae.
Suborder Passeres.

b) Members of the pair touch at the ventral midline, not necessarily at insertion.
Cotingidae (part): *Iodopleura, Attila, Casiornis, Laniocera, Rhytipterna, Pachyramphus, Platypsaris.*
Pipridae (part): *Pipra, Chiroxiphia, Corapipo, Manacus, Ilicura.*
Tyrannidae (part): *Agriornis, Xolmis, Muscisaxicola, Lessonia, Neoxolmis, Ochthoeca, Sayornis, Colonia, Gubernetes, Yetapa, Knipolegus, Phaeotriccus, Entotriccus, Lichenops, Muscipipra, Fluvicola, Arundinicola, Pyrocephalus, Muscigralla, Satrapa, Machetornis, Muscivora, Tyrannus, Empidonomus, Megarhynchus, Tyrannopsis, Tolmarchus, Myiarchus* (part), *Nutallornis, Myiochanes, Blacicus, Empidonax, Aechmolophus, Cnemotriccus, Mitrephanes, Pyrrhomyias, Myiophobus, Platyrinchus, Tolmomyias* (part), *Pogonotriccus, Leptotriccus, Phylloscartes, Capsiempis, Euscarthmus, Pseudocolopteryx, Habrura, Tachuris, Stigmatura, Corythopis, Serpophaga, Inezia, Mecocerculus, Colorhamphus, Elaenia, Camptostoma, Phyllomyias, Tyranniscus, Microtriccus, Leptopogon, Mionectes, Pipromorpha.*
Oxyruncidae.

b. M. sternotrachealis.

i. Mode of insertion.

a) Directly on the lateral surface of the trachea.
Eurylaimidae (part): *Cymbirhynchus, Psarisomus, Calyptomena.*

Cotingidae (part) : *Heliochera, Cotinga, Xipholena, Carpodectes, Attila, Casiornis, Lipaugus, Pachyramphus, Perissocephalus.*
Pipridae (part) : *Corapipo, Schiffornis.*
Tyrannidae (part) : *Agriornis, Ochthoeca, Sayornis, Yetapa, Arundinicola, Pyrocephalus, Muscigralla, Satrapa, Legatus, Sirystes, Myiozetetes* (part), *Pitangus, Myiarchus, Eribates, Nuttallornis, Blacicus, Empidonax, Cnemotriccus, Mitrephanes, Terenotriccus, Myiobius, Pyrrhomyias, Myiophobus, Tolmomyias, Rhynchocyclus, Todirostrum, Lophotriccus, Colopteryx, Myiornis, Hemitriccus, Pogonotriccus, Leptotriccus, Phylloscartes, Euscarthmus, Tachuris, Spizitornis, Stigmatura, Corythopis, Serpophaga, Mecocerculus, Colorhamphus, Elaenia* (part), *Suiriri, Sublegatus, Phaeomyias, Camptostoma, Tyranniscus, Tyrannulus, Microtriccus, Leptopogon, Pipromorpha.*
Phytotomidae.
Pittidae (part).
Philepittidae.
Acanthisittidae.
Suborder Menurae.
Suborder Passeres.

b) In continuity with M. tracheolateralis.
Eurylaimidae (part) : *Smithornis, Eurylaimus.*
Cotingidae (part) : *Euchlornis, Rhytipterna, Querula, Cephalopterus, Gymnoderus, Conioptilon, Rupicola.*
Pipridae (part) : *Piprites, Chiroxiphia, Manacus.*
Tyrannidae (part) : *Colonia, Onychorhynchus, Oncostoma, Euscarthmornis.*
Pittidae (part).
Oxyruncidae.

c) On the membranous sheath of M. tracheolateralis.
Pipridae (part) : *Pipra.*
Tyrannidae (part) : *Aechmolophus.*

d) By a broad tendinous sheet to the trachea.
Cotingidae (part) : *Pyroderus.*

e) Part of each muscle attached directly to the trachea; the remainder continuous with M. tracheolateralis.
Cotingidae (part) : *Phoenicircus, Iodopleura, Platypsaris.*
Tyrannidae (part) : *Muscipipra, Myiodynastes, Myiozetetes, Pitangus, Nesotriccus, Aphanotriccus, Platyrinchus, Pseudocolopteryx, Elaenia, Leptopogon, Mionectes.*

f) Part of each muscle attached directly to the trachea; the remainder attached to the membranous sheath surrounding M. tracheolateralis.
Pipridae (part) : *Ilicura.*
Tyrannidae (part) : *Xolmis, Neoxolmis, Gubernetes, Lichenops, Empidonomus, Tolmarchus, Myiochanes, Inezia.*

g) Part of each muscle continuous with M. tracheolateralis; the remainder inserting on the membranous sheath surrounding M. tracheolateralis.
Cotingidae (part) : *Laniocera.*

Tyrannidae (part): *Muscisaxicola, Lessonia, Phaeotriccus, Entotriccus.*

h) Three fasciculi: one continuous with M. tracheolateralis; one attached directly to the lateral surface of the trachea; one inserting on the membranous sheath of M. tracheolateralis.
Tyrannidae (part): *Knipolegus, Machetornis, Muscivora, Tyrannus, Megarhynchus, Conopias, Elaenia* (part).

i) By a diffuse tendon to the surface of the intrinsic muscle.
Cotingidae (part): *Procnias.*

2. Intrinsic muscles.
   a. Number present.
      i. None.
      Suborder Eurylaimi.
      Suborder Tyranni (part):
      Cotingidae (part): *Phoenicircus, Heliochera, Cotinga, Xipholena, Carpodectes, Euchlornis, Lipaugus, Tityra, Querula, Pyroderus, Cephalopterus, Perissocephalus, Gymnoderus, Conioptilon, Rupicola.*
      Pipridae (part): *Piprites, Manacus.*
      Tyrannidae (part): *Machetornis, Terenotriccus, Myiobius, Pyrrhomyias, Onychorhynchus, Tyranniscus* (part).
      Phytotomidae.
      Pittidae.
      Philepittidae.
      Acanthisittidae.
      ii. One pair.
      Cotingidae (part): *Iodopleura, Attila, Casiornis, Laniocera, Rhytipterna, Pachyramphus, Platypsaris, Procnias.*
      Pipridae (part): *Pipra, Chiroxiphia, Ilicura, Schiffornis.*
      Tyrannidae (part): all except those with none (above) and those with two pairs (below).
      Oxyruncidae.
      iii. Two pairs.
      Pipridae (part): *Corapipo.*
      Tyrannidae (part): *Ochthoeca, Legatus, Myiozetetes, Nuttallornis, Tolmomyias* (part), *Oncostoma, Euscarthmornis, Lophotriccus, Colopteryx, Myiornis, Hemitriccus, Leptotriccus, Phylloscartes, Pseudocolopteryx, Elaenia, Suiriri, Phaeomyias, Camptostoma.*
      iv. Three pairs.
      Suborder Menurae.
      v. Four pairs.
      Suborder Passeres.
   b. Properties of the intrinsic muscles (in birds possessing one pair), or of the ventral intrinsic muscles (in birds possessing two pairs). Properties in birds with three and four pairs are not handled in this summary.
      i. Region of origin.
         a) Adjacent to the ventral midline or by a raphe (indicated by "r") to the ventral midline, or both.
         Cotingidae (part): *Iodopleura.*

Tyrannidae (part): *Sayornis* (r), *Knipolegus, Phaeotriccus, Arundinicola* (r), *Muscigralla* (r), *Legatus, Myiozetetes, Nesotriccus, Nuttallornis* (r), *Myiochanes* (r), *Blacicus* (r), *Empidonax* (r), *Aechmolophus* (r), *Aphanotriccus* (r), *Rhynchocyclus* (r), *Pogonotriccus* (r), *Leptotriccus, Euscarthmus* (r), *Pseudocolopteryx* (r), *Stigmatura* (r), *Corythopis* (r), *Inezia* (r), *Elaenia* (part, r), *Suiriri* (r), *Phaeomyias* (r), *Camptostoma, Phyllomyias, Tyranniscus* (part), *Microtriccus, Leptopogon.*
Oxyruncidae.

b) Adjacent to the ventral midline and on the ventral and ventrilateral surfaces of one or more elements.
Cotingidae (part): *Attila, Casiornis, Laniocera, Rhytipterna.*
Pipridae (part): *Ilicura.*
Tyrannidae (part): *Agriornis, Xolmis, Neoxolmis, Entotriccus, Fluvicola, Sirystes, Myiarchus, Eribates, Capsiempis, Elaenia* (part).

c) Directly on the ventral region of one or more elements.
Tyrannidae (part): *Pyrocephalus* (part), *Platyrinchus, Oncostoma, Hemitriccus, Tachuris, Colorhamphus, Mionectes, Pipromorpha.*

d) Directly on the ventral and ventrilateral surfaces of one or more elements.
Pipridae (part): *Pipra, Chiroxiphia.*
Tyrannidae (part): *Lessonia, Ochthoeca, Pyrocephalus* (part), *Tolmomyias, Oncostoma, Euscarthmornis, Colopteryx, Myiornis, Phylloscartes, Spizitornis.*

e) Directly on the ventrilateral surfaces of one or more elements.
Cotingidae (part): *Pachyramphus, Platypsaris.*

f) Directly on the ventrilateral, lateral and dorsolateral surfaces of one or more elements.
Tyrannidae (part): *Tyrannus, Empidonomus, Myiodynastes, Conopias, Tyrannopsis, Tolmarchus.*

g) Directly on the ventral, ventrilateral and lateral surfaces of one or more elements.
Tyrannidae (part): *Gubernetes, Yetapa, Muscivora, Pitangus, Habrura, Serpophaga, Mecocerculus.*

h) Directly on the lateral surfaces of one or more elements.
Pipridae (part): *Corapipo, Schiffornis.*
Tyrannidae (part): *Tolmomyias* (part), *Todirostrum.*

i) Adjacent to the ventral midline and along the ventral, ventrilateral and lateral surfaces of one or more elements.
Tyrannidae (part): *Colonia, Cnemotriccus, Tyrannulus.*

j) Adjacent to the ventral midline (or by a raphe to the midline) and on the ventral, ventrilateral, lateral and dorsolateral surfaces of one or more elements.
Tyrannidae (part): *Lichenops, Pitangus* (part), *Myiophobus.*

k) Completely encircling the trachea on several elements.
Cotingidae (part): *Procnias.*

ii. Element and region of insertion.

a) A-1, dorsal 1/5th of the element.
Tyrannidae (part): *Myiozetetes, Platyrinchus.*

b) A-1, middle region (1/5 - 1/3 the length of the element).
Tyrannidae (part): *Agriornis, Xolmis, Colonia, Gubernetes, Knipolegus, Entotriccus, Muscipipra, Fluvicola, Satrapa, Sirystes, Myiarchus, Eribates, Nuttallornis, Myiochanes, Empidonax, Mitrephanes, Rhynchocyclus, Tolmomyias.*

c) A-1, ventral end, terminally.
Pipridae (part): *Corapipo.*

d) A-1, ventral 1/3 - 1/2.
Cotingidae (part): *Casiornis, Rhytipterna.*
Tyrannidae (part): *Muscisaxicola, Lessonia, Ochthoeca, Phaeotriccus, Muscigralla, Blacicus, Aechmolophus, Pseudocolopteryx, Elaenia* (part).

e) A-1, ventral 2/3.
Tyrannidae (part): *Neoxolmis, Sayornis, Aphanotriccus.*

f) A-1/B-1 membrane.
Cotingidae (part): *Attila, Laniocera.*
Tyrannidae (part): *Yetapa, Arundinicola, Pyrocephalus, Cnemotriccus, Leptotriccus, Phylloscartes, Habrura, Spizitornis, Stigmatura, Corythopis, Elaenia* (part), *Phyllomyias, Tyrannulus.*

g) B-1, dorsal 1/5.
Cotingidae (part): *Iodopleura, Platypsaris.*
Tyrannidae (part): *Empidonomus, Legatus, Conopias, Pitangus* (part), *Platyrinchus, Oncostoma, Euscarthmornis, Lophotriccus, Colopteryx, Myiornis, Hemitriccus, Pogonotriccus, Inezia, Elaenia, Suiriri, Phaeomyias, Camptostoma, Tyranniscus* (part), *Microtriccus, Leptopogon.*

h) B-1, center.
Cotingidae (part): *Pachyramphus.*
Pipridae (part): *Schiffornis.*
Tyrannidae (part): *Tolmomyias, Todirostrum, Euscarthmus, Tachuris, Colorhamphus.*
Oxyruncidae.

i) B-1, ventral 1/6.
Tyrannidae (part): *Mionectes.*

j) B-1, entire length.
Pipridae (part): *Ilicura.*

k) B-1/B-2 membrane, dorsolateral region.
Tyrannidae (part): *Tolmarchus.*

l) On more than one element and/or membrane.
A-1 and B-1, dorsolaterally. Tyrannidae: *Muscivora, Nesotriccus, Myiophobus.*
A-1 and B-1, ventrilaterally. Tyrannidae: *Pipromorpha.*
A-1/B-1 membrane and B-1, laterally. Tyrannidae: *Serpophaga.*
A-1, B-1, and B-1/B-2 membrane. Tyrannidae: *Tyrannus.*
A-1/A-2 membrane, A-1, B-1, and B-1/B-2 membrane, dorsolaterally. Tyrannidae: *Myiodynastes.*
A-1, A-1/B-1 membrane, B-1/B-2 membrane, and B-2, dorsolaterally. Tyrannidae: *Megarhynchus, Pitangus* (part).

A-1/B-1 membrane, B-1, B-1/B-2 membrane, B-2, nearly the entire areas of these elements; anterior edges of the internal tympaniform membranes. Cotingidae: *Procnias.*

iii. Fiber direction.

a) Approximately parallel to the bronchial axis.
Cotingidae (part) : *Procnias.*
Pipridae (part) : *Pipra, Chiroxiphia, Schiffornis.*
Tyrannidae (part): *Tolmomyias* (part), *Todirostrum, Spizitornis, Mecocerculus.*

b) Ventral fibers oblique; lateral or dorsal ones approximately parallel to the bronchial axis.
Cotingidae (part) : *Attila, Casiornis, Laniocera, Rhytipterna.*
Tyrannidae (part) : *Agriornis, Xolmis, Muscisaxicola, Lessonia, Neoxolmis, Ochthoeca, Colonia, Gubernetes, Yetapa, Knipolegus, Entotriccus, Lichenops, Muscipipra, Fluvicola, Pyrocephalus* (part), *Satrapa, Muscivora, Tyrannus, Empidonomus, Legatus, Sirystes, Myiodynastes, Megarhynchus, Conopias, Pitangus, Myiozetetes, Tolmarchus, Myiarchus, Eribates, Nesotriccus, Cnemotriccus, Myiophobus, Tolmomyias* (part), *Capsiempis, Habrura, Serpophaga, Elaenia* (part), *Tyrannulus.*

c) All fibers oblique (anteroventrimedial-posterodorsolateral).
Cotingidae (part) : *Iodopleura, Pachyramphus, Platypsaris.*
Pipridae (part) : *Ilicura.*
Tyrannidae (part) : *Sayornis, Phaeotriccus, Arundinicola, Pyrocephalus* (part), *Muscigralla, Nuttallornis, Myiochanes, Blacicus, Empidonax, Aechmolophus, Mitrephanes, Aphanotriccus, Platyrinchus, Rhynchocyclus, Oncostoma, Euscarthmornis, Lophotriccus, Colopteryx, Myiornis, Hemitriccus, Pogonotriccus, Leptotriccus, Phylloscartes, Euscarthmus, Pseudocolopteryx, Tachuris, Stigmatura, Corythopis, Inezia, Colorhamphus, Elaenia* (part), *Suiriri, Sublegatus, Phaeomyias, Camptostoma, Tyranniscus* (part), *Microtriccus, Leptopogon, Mionectes, Pipromorpha.*
Oxyruncidae.

c. Properties of the lateral or dorsal intrinsic muscle, in birds possessing two pairs.

i. Region of origin.

a) On the lateral surface of one or more elements.
Pipridae (part) : *Corapipo.*
Tyrannidae (part) : *Legatus, Myiozetetes, Oncostoma, Euscarthmornis, Lophotriccus, Colopteryx, Myiornis, Leptotriccus, Phylloscartes, Pseudocolopteryx.*

b) On the dorsolateral surface of one or more elements.
Tyrannidae (part): *Nuttallornis, Tolmomyias* (part), *Hemitriccus, Elaenia, Suiriri, Phaeomyias, Camptostoma.*

c) Near the dorsal midline of two or more elements.
Tyrannidae (part) : *Ochthoeca.*

ii. Element and region of insertion.

a) A-1, dorsal end.
Pipridae (part) : *Corapipo.*

b) A-1, center.
Tyrannidae (part): *Ochthoeca, Nuttallornis, Tolmomyias, Pseudocolopteryx, Elaenia* (part), *Suiriri, Phaeomyias.*

c) A-1, ventral 1/3.
Tyrannidae (part): *Elaenia* (part).

d) A-1/B-1 membrane, center.
Tyrannidae (part): *Phylloscartes, Leptotriccus.*

e) B-1, dorsal end.
Tyrannidae (part): *Oncostoma, Euscarthmornis, Lophotriccus, Colopteryx, Myiornis, Hemitriccus.*

f) B-1, center.
Tyrannidae (part): *Camptostoma.*

g) B-1, ventral 1/2.
Tyrannidae (part): *Legatus, Myiozetetes.*

MAJOR STRUCTURAL DIVISIONS.

The preceding detailed morphological summary does not fully express the broad structural groups into which passerine syringes may be divided. The following groups comprise birds whose syringes share a number of features not found in other groups. To these features are added others that characterize the group, but are shared with some other groups. The outline is not presented as a taxonomic classification; it merely reflects the different levels of structural complexity found in the passerine syrinx.

Division I

Limited modification of tracheobronchial region. Little or no fusion of A-elements. Pessulus present. No internal cartilages. Mm. tracheolaterales usually narrow or medium in width; insert on divided or double A-element. Mm. sternotracheales usually narrow, insertion variable. No intrinsic muscles. Some groups placed in this division do not conform with above in certain characteristics, but are placed here because of general conformity.

Suborder Eurylaimi.

Eurylaimidae. (Mm. tracheolaterales insert on a complete element in *Smithornis.*)

Suborder Tyranni.

Superfamily Tyrannoidea.

Cotingidae (part): all except *Attila, Casiornis, Rhytipterna, Procnias, Laniocera, Pachyramphus, Platypsaris, Iodopleura.*

Pipridae (part): *Piprites.*

Tyrannidae (part): *Terenotriccus, Myiobius, Pyrrhomyias, Onychorhynchus.* (Internal cartilages present in *Myiobius.*)

Phytotomidae.

Pittidae (pessulus lacking in most species).

Philepittidae (internal cartilages present in *Neodrepanis*).

Acanthisittidae. Much fusion of A-elements; Mm. tracheolaterales insert on a complete element; internal cartilages present in *Acanthisitta.*

Division II

Lower trachea dorsoventrally compressed; elements in compressed region attenuated and sometimes lacking, compressed region thus forming "windows" (Membranae tracheales). Fusion of A-elements, when present, always anterior to Membranae. Lateral bars or plates (Processi vocales) present. Pessulus invariably lacking. Mm. tracheolaterales variable, inserting either on Processi, on elements anterior to Membranae, or both. Mm. sternotracheales insert on anterior ends of Processi and/or on elements anterior to Membranae. Intrinsic muscles consist of none, one, or two pairs; if present, they originate on elements anterior to Membranae and insert on Processi (rarely, also on elements posterior to Membranae).

Suborder Tyranni.

Superfamily Furnarioidea.

Subdivision A.

Processi large, straight, thick bars. No intrinsic muscles.

Formicariidae (part) : *Formicarius, Chamaeza, Grallaria, Conopophaga.*

Rhinocryptidae (part) : *Teledromas.*

Subdivision B.

Processi small soft plates anchored to underlying elements by strong fibrous sheets. Each M. sternotrachealis inserts by two fasciculi, one to Processus, other to dorsolateral surfaces of several elements immediately anterior to Membranae. One pair of intrinsic muscles present (Mm. vocales ventrales) ; originates near ventral midline and/or ventrilateral surfaces of several elements immediately anterior to Membranae; insert on anterodorsal regions of Processi.

Formicariidae (part) : all except *Formicarius, Chamaeza, Grallaria* and *Conopophaga.*

Subdivision C.

Processi nearly straight, broad at ends and narrow in middle. Mm. sternotracheales insert on flared anterior ends of Processi. One pair of intrinsic muscles present (Mm. vocales dorsales) ; originates laterally on elements immediately anterior to Membranae; inserts on anteroventral or ventral regions of Processi.

Rhinocryptidae (part) : all except *Teledromas.*

Subdivision D.

Processi nearly straight, usually broad at ends and narrow in middle (as in Subdivision C.) ; rarely of uniform width. Insertion of Mm. tracheolaterales several elements removed from Membranae tracheales. Mm. sternotracheales insert on anterior ends of Processi. Two pairs of intrinsic muscles present (Mm. vocales ventrales and Mm. vocales dorsales) ; originate on anterior edge of drum; insert on Processi.

Furnariidae (part) : all except *Geositta.*

Subdivision E.

Processi broad at bases; prominent "horns" extend from middle of dorsal and ventral sides. Fusion of two or more A-elements usually present, always including one

immediately anterior to Membranae. Mm. tracheolaterales insert on anterior edge of drum thus formed. Mm. sternotracheales as in Subdivision D, above. Two pairs of intrinsic muscles present (Mm. vocales ventrales and Mm. vocales dorsales); originate as in Subdivision D; insert on ventral and dorsal "horns" of Processi, respectively.

Dendrocolaptidae.

Furnariidae (part): *Geositta.*

Division III

Lower trachea roughly cylindrical, with or without fusion of A-elements. Pessulus present or absent. Internal cartilages present (except in Subdivision A). Mm. tracheolaterales frequently, but not always, in contact with each other at ventral midline; usually insert on one or more A-elements at level of A-4 or above. Mm. sternotracheales variable in type of insertion. When two pairs of intrinsic muscles are present, Mm. sternotracheales usually insert dorsal or anterodorsal to origins of both. Intrinsic muscles number one or two pairs. Within this division several subdivisions are recognized, but not all members of the division are included in them, as morphological variation is complex and frequently clinal.

Suborder Tyranni

Superfamily Tyrannoidea

Cotingidae (part): *Attila, Laniocera, Platypsaris, Iodopleura, Casiornis, Rhytipterna, Pachyramphus.*

Pipridae (part): *Pipra, Chiroxiphia, Corapipo, Schiffornis.*

Tyrannidae (part): all except *Machetornis, Terenotriccus, Myiobius, Pyrrhomyias, Onychorhynchus.*

Subdivision A.

Internal cartilages absent. Pessulus present. Rigid cylindrical drum formed of fused A-elements. One pair of intrinsic muscles.

Pipridae (part): *Pipra, Chiroxiphia.*

Subdivision B.

Fusion, when present, involves only two or three A-elements. Pessulus present or absent. Two pairs of internal cartilages present, dorsal and larger pair J- or J-shaped. One pair of intrinsic muscles (Mm. obliqui ventrales).

Cotingidae (part): *Attila, Casiornis, Rhytipterna, Laniocera.*

Tyrannidae (part): *Myiarchus, Eribates.*

Subdivision C.

Fusion, when present, incomplete (except in *Empidonomus*), but lower four or five A-elements always closely fitted. A-2 double. A-2, A-3, and sometimes A-4 with sharp corners in dorsomedial region. B-1 and B-2 fused at their ventral ends (except in *Pitangus,* in which B-3 and B-4 are fused). Pessulus present or absent (sometimes both in same genus). Internal cartilages straight or J-shaped. Mm. sternotracheales thick, usually with multiple insertions. One pair of intrinsic muscles (Mm. obliqui ventrales); short, broad and extremely thick, not touching at ventral midline; orig-

inating on ventrilateral, lateral and dorsolateral surfaces of several elements; having multiple dorsolateral insertion.

Tyrannidae (part): *Muscivora, Tyrannus, Empidonomus, Tyrannopsis, Myiodynastes, Megarhynchus, Conopias, Tolmarchus, Pitangus.*

Subdivision D.

Little or no fusion of elements, but divided A-elements usually closely fitted. Lower three or four A-elements divided. Pessulus present or absent; when present, free at one end. Cartilaginous plug or transverse bridge in dorsal interbronchial region. Internal cartilages short rounded triangles or straight bars, fused to cartilaginous plug. Mm. tracheolaterales extend under intrinsic muscles to insert on A-1 and/or A-2. Mm. sternotracheales insert directly on trachea (except in *Myiochanes*). One pair of intrinsic muscles present, except in *Nuttallornis*, which has two pairs. Mm. obliqui ventrales originate on midventral raphe (except in some specimens of *Sayornis*, in which pair of muscles are ventrally continuous) and insert on A-1.

Tyrannidae (part): *Sayornis, Nuttallornis, Myiochanes* [= *Contopus*], *Blacicus, Empidonax, Aphanotriccus, Mitrephanes.*

Subdivision E.

Three or more A-elements fused, completely or partially, into rigid drum. Pessulus present and fused to drum. Internal cartilages consist of narrow straight or curved bars bearing thin semicircular ventral extensions (except in *Suiriri* and *Phaeomyias*). Mm. sternotracheales insert directly (rarely, also with continuity with Mm. tracheolaterales). Two pairs of intrinsic muscles present (except in *Microtriccus*). Ventral pair (Mm. obliqui ventrales) originates on a midventral raphe which is attached to drum; insert directly on A-1 or on A-1/B-1 membrane, or by a tendon to dorsal fifth of B-1. Lateral pair (Mm. obliqui laterales) originates ventrilaterally and laterally and inserts directly on A-1.

Tyrannidae (part): *Elaenia, Suiriri, Phaeomyias, Camptostoma, Microtriccus.*

Subdivision F.

Lower trachea characterized by the presence of many dorsally incomplete elements, each with a rather wide opening at the dorsal midline. Pessulus present; bends anteriad at dorsal surface of syrinx, extending up dorsal midline in openings of dorsally incomplete elements. Mm. sternotracheales thick, insertion variable. Two pairs of intrinsic muscles usually present. Ventral pair (Mm. obliqui ventrales) originate ventrally and interdigitate at origin; insert subterminally on dorsal end of B-1. Lateral pair (Mm. obliqui laterales) originates immediately posterior to the insertion of Mm. sternotracheales and inserts dorsally adjacent to Mm. obliqui ventrales.

Tyrannidae (part): *Oncostoma, Euscarthmornis, Lophotriccus, Colopteryx, Myiornis, Hemitriccus.*

Division IV

Lower three A-elements divided, consisting of thick round bars, slightly curved and flattened at dorsal ends. Pessulus present (except in the Alaudidae) and fused to A-4 at both ends. No internal cartilages. Mm. tracheolaterales insert on the anterior

surface of the syringeal aponeurosis and on the lateral, dorsolateral and dorsal surfaces of the trachea. Mm. sternotracheales insert on the lateral surface of the trachea, posterior to syringeal aponeurosis and between the dorsal and ventral long intrinsic muscles. Three or four pairs of intrinsic muscles present, always including one pair of ventral long muscles (Mm. bronchotracheales antici) and one pair of dorsal long muscles (Mm. bronchotracheales postici); originate on the posterior surface of syringeal aponeurosis and on lateral and dorsolateral surfaces of the trachea; insert on respective ends of A-1 and A-2.

Suborder Menurae.

Suborder Passeres

Subdivision A.

No fusion of A-elements. Three pairs of intrinsic muscles present, ventral and dorsal pairs of long muscles and pair of short dorsal muscles.

Suborder Menurae.

Subdivision B.

Elements A-4 through A-7 (rarely, through A-8) fused, forming drum. Four pairs of intrinsic muscles present, those found in Subdivision A. and pair of short ventral muscles.

Suborder Passeres (Pessulus lacking in Alaudidae).

HISTORY OF PASSERINE CLASSIFICATION

In the eighteenth century the order Passeriformes was considered to include virtually all terrestrial and arboreal birds except the birds of prey, the game birds, and the large cursorial forms. The increase of anatomical knowledge in the nineteenth century resulted in the gradual narrowing of the order to its modern limits.

Nitzsch (1829, 1840), basing his conclusions on the anatomy of the carotid arteries, pterylosis, and syrinx, separated several other orders from the passerines. Sundevall (1872) pointed out that certain families, which include only the hoopoes (Upupidae) and most of the modern Passeriformes, lack the connecting vinculum between certain tendons of the leg M. flexor halucis longus and M. flexor perforans digitorum. Keyserling and Blasius (1839) observed that all passerines in which the syrinx is elaborately muscled (i.e., the oscines) possess bilaminate planta tarsi. Müller (1847) viewed the passerines in the broad sense and his contribution was to the subdivisions of the order, rather than to its boundaries.

Cabanis and Heine (1859) treated the Passeriformes with essentially the same classification as is used today, combining the ideas of Nitzsch, Keyserling and Blasius, and Müller. Lacking knowledge of the internal anatomy of many forms, Cabanis and Heine were sometimes misled by external appearances. They included the pittas with some of the antbirds in their Hypocnemidae, the lyrebirds (*Menura*) with the tapaculos (Rhinocryptidae), and the nonpasserine todies (Coraciiformes) with the Tyrannidae. Their family mergers—the modern Furnariidae and Dendrocolaptidae in a single family Anabatinae and the modern Cotingidae and Pipridae in a family Ampelidae—were endorsed by many subsequent authors. Their arrangement of genera in the tyrant flycatchers, cotingas, and manakins formed the basis for the later arrangements of Sclater (1888), von Berlepsch (1905) and Hellmayr (1927).

More than any other man, A. H. Garrod was responsible for the modern boundaries and subdivisions of the Passeriformes. He defined the order (1873, 1876) in terms of the short colic caeca, nude oil gland, aegithognathous palate, the absence of M. ambiens in the knee, and the form of the tendon of M. tensor patagi brevis. He separated the broadbills (Eurylaimidae) from the rest of the order on the basis of their plantar vinculum and non-bifurcate Manubrium sterni [= *Spina sternalis*]. On the basis of syringeal muscle attachments, he divided the remaining passerines into Acromyodae and Mesomyodi. The former were further divided into "Normales" (oscines) and "Abnormales" (Menurae) depending on the number of syringeal muscles. He divided the Mesomyodae, which were synonymous with the modern suborder Tyranni, into Tracheophonae (the superfamily Furnarioidea) and Oligomyodae (Tyrannoidea) on the Müllerian basis. Within his Tracheophonae he separated the Furnariidae from the Dendrocolaptidae on the basis of nasal osteology. Garrod also attempted, with some success, to separate the Pipridae and Cotingidae (except *Rupicola*) from the other Tyrannoidea on the basis of the dominant artery of the thigh. He removed the pittas from the antbirds after a study of the syrinx and skull and placed them in his Oligomyodae.

After Garrod's death in 1879, his work was continued by his student, W. A. Forbes, who studied several genera about which little was known. On the basis of syrinx, tarsal scutellation, and the osteology of the sternum and nasal bones, he established the family Conopophagidae (1881) for the genera *Conopophaga* and *Corythopis*. The family was subsequently submerged by Ames, Heimerdinger and Warter (1968). The New Zealand "wrens," *Xenicus* and *Acanthisitta*, were removed from the oscines by Forbes (1882a) and placed in the Oligomyodae as the family Xenicidae (now Acanthisittidae). He defined the Philepittidae (1880b) on the basis of their syringeal structure, non-bifurcate Manubrium sterni, and lack of a plantar vinculum. By 1885 the relationships and limits of all the non-oscine families were understood essentially as they are today.

P.L. Sclater (1888) accepted most of the ideas of Garrod and Forbes, but separated the broadbills at a lower level of the system. His first and second divisions of the order were based on syringeal structure. The Acromyodi and Mesomyodi were the same as in Garrod's classification, except that the Eurylaimidae were included in the Mesomyodi. The Mesomyodi were divided into Oligomyodi and Tracheophonae, as was done by Garrod. Sclater further divided the Oligomyodi on the basis of the plantar tendons, placing the broadbills in the Desmodactyli and the rest, comprising the modern Tyrannoidea, in the Eleutherodactyli. Sclater relied on tarsal scutellation, the degree of syndactyly, and bill shape to define the eight families of his Eleutherodactyli. Four subfamilies of the Tyrannidae were based on the proportions of the legs and feet, on habitat and coloration, and on the degree of development of rictal bristles.

Hans Gadow (in Gadow and Selenka, 1893) relied heavily on the syrinx in classifying the Passeriformes. One half of the order, designated "Anisomyodae" because the syringeal muscles were thought to be dorsoventrally asymmetrical, included the Subclamatores (Eurylaimidae) and Clamatores (Pittidae, Xenicidae, Tyrannidae, Formicariidae, and Pteroptochidae). In the Tyrannidae were two subfamilies: Tyranninae (including the manakins) and Cotinginae. The Conopophigidae of other authors were included by Gadow in the Formicariidae; the Furnariidae and Dendrocolaptidae were in his Pteroptochidae. The other half of the Passeriformes, which he called "Diacromyodae" because the syringeal muscles are attached to both ends of the elements, contained the "Suboscines" (*Menura*) and Oscines.

Ridgway (1901-1907) divided the Passeriformes into two suborders on the basis of the plantar vinculum. The Eurylaimi alone constituted his Desmodactyli, all other groups being in the Eleutherodactyli. In the latter suborder he recognized three superfamilies: Clamatores (Tyranni), Pseudoscines (Menurae), and Oscines. The Clamatores were divided into Tracheophonae and Oligomyodae, as they were by Garrod. Ridgway relied strongly on the type of tarsal scutellation to determine family boundaries, often contrary to his better judgment.

Pycraft (in Ridgway, 1907, part IV, p. 332) differed from most of his contemporaries in his arrangement of the passerines. He recognized four suborders, based largely on syringeal structure. One of these contained the Eurylaimidae, Cotingidae and Philepittidae, another the "Tracheophonae" (Furnariodea), a third the Tyrannidae (and presumably the Pipridae) and Pittidae, the fourth "the rest of the passeres." The tracheophonae were divided into three subgroups based on the nasal bones and the number of notches in the metasternum.

Von Ihering (1904) attempted to subdivide the Tyrannidae on a non-morphological basis, using primarily the form of the nest, egg color, and zoogeography. He altered the subfamilies employed by Sclater, splitting some and merging others. Moreover, he speculated that the common ancestor of the tyrant flycatchers and manakins was a small olive bird with a "somewhat compressed and bristled bill and pronounced syndactyly," like certain of the modern Elaeniinae. Although he dealt with only about a third of the Tyrannidae, von Ihering introduced new taxonomic criteria in a family in which feeding adaptations had been overemphasized as taxonomic characters. His ideas had a profound effect on subsequent classifiers, particularly von Berlepsch and Hellmayr.

Von Berlepsch (1905) attempted to arrange the Tyrannidae "according to their natural relationships." Although he followed many of von Ihering's suggestions, he relied principally on external structural characters and on intuition.

Hellmayr (1924-38) produced the most recent complete revision of the New World passerines. He followed Garrod's classification with regard to major subdivisions, but employed non-anatomical names for the subdivisions. He recognized two suborders in the Western Hemisphere passerines: the Tyranni (equivalent to Garrod's Mesomyodi) and Passeres (Acromyodi normales). The two superfamilies of the Tyranni, the Furnarioidea and Tyrannoidea, were precisely equivalent to the Tracheophonae and Oligomyodi as far as the included families were concerned. Hellmayr disagreed with Sclater and with Ridgway on the systematic positions of many genera. Where Ridgway attempted to adhere to rigid structural criteria, Hellmayr was more flexible. Nevertheless, he regarded Ridgway's opinions highly and the family allocations of many genera show Ridgway's reliance on tarsal scutellation, rather than Hellmayr's intuition. In arranging the Tyrannidae and Pipridae he used beak shape, wing shape and tarsal scutellation, in conjunction with an assortment of other characters, to establish intergeneric relationships.

Peters (1951) and Wetmore (1960) agreed with Hellmayr on the subordinal divisions of the Passeriformes. Their classification of the order was the result of more than a century of accumulated anatomical and behavioral investigation by scores of ornithologists. Despite this large amount of knowledge there are many unsolved questions in passerine systematics. The allocation of the three Old World families of ground dwelling birds, Pittidae, Philepittidae, and Acanthisittidae, to the Tyranni is based on scanty evidence. The family boundaries of the Tyrannidae, Pipridae, and Cotingidae are greatly in need of reëvaluation, for no one has examined the taxonomic characters of these groups since Ridgway (1907).

Inasmuch as the major subdivisions of the Passeriformes, as presently understood, are based on syringeal morphology, it is singularly appropriate to examine the classification of the order in the light of the data of the present investigation.

COMMENTS ON THE ADJECTIVES OF SYRINGEAL MORPHOLOGY

INTRODUCTION.

Throughout the history of syringeal study anatomists have named the parts of the syrinx on the basis of assumed function or of similarity to the respiratory systems of other animals. A re-examination of the classical adjectives now appears warranted, with particular attention to the series of "-myodean" words introduced by Müller, Huxley, and others, and to the terms "tracheal" and "bronchial."

THE "-MYODEAN" ADJECTIVES.

Of the eight terms ending in "-myodean" two, "polymyodean" and "oligomyodean," refer to the number of intrinsic muscles, the others to the position of their insertion. Müller (1847) applied the term "Passerini Polymyodi" to the birds with complex syringes (oscines), but stated that the term was only descriptive, not intended to denote a taxonomic division of the order. Huxley (1867) used the term "oligomyodi" to designate those passerines treated by Müller as "Picarii." In their original sense the two words served to describe in approximate terms two of the syringeal types on which the separation of the oscines from the other passerines was based. The polymyodean syrinx has four or five pairs of intrinsic muscles, according to Müller. More important, they act on the ends of two or more cartilaginous elements. Multiplicity of action was stressed more strongly by Müller than the number of muscles. He placed *Menura,* which he believed to have only two pairs of intrinsic muscles, in the "Polymyodi" group because the insertions of the muscles are widely separated dorsoventrally. In the Müllerian sense, the terms "polymyodean" and "oligomyodean" are not wholly appropriate, being names based on muscle numbers, but employed on the basis of muscle attachments. Subsequent use of the terms as taxonomic names (Sclater, 1888; Ridgway, 1901-1907) was even less appropriate, for only a few of the birds involved had been studied anatomically.

Recognizing the weakness in the application of poly- and oligomyodean, Garrod (1876) coined two new words intended to describe more accurately the conditions present. He referred to the condition found in Müller's "Polymyodi" as "acromyodean," and to that in Müller's "Picari" (the Oligomyodi of Huxley) as "mesomyodean." In Garrod's outline of passerine classification the "Mesomyodi" and "Acromyodi" were the first subdivisions of the order. Garrod included in his Mesomyodi the groups placed by Müller in the third major division, Tracheophones.

Gadow and Selenka (1893) introduced more detailed modifications of "acromyodean": the words "anisomyodean" and "an-," "cat-," and "diacromyodean." They

defined various types of musculature in terms of dorsoventral symmetry, or lack of it, and of the point of insertion. Although the words are valid for describing many syringeal types, they are inadequate to describe the broad array of muscle forms found in the Tyrannoidea. In most applications the specialized positional terms of Garrod and of Gadow and Selenka oversimplify the actual situations, creating false impressions about similarities.

THE TERMS "TRACHEAL" AND "BRONCHIAL".

Included in the description of the anatomy of a species one often finds the statement that the syrinx is "tracheo-bronchial" or "tracheal." The application of these terms is based on the assumption that the trachea or the bronchi may be distinguished by the nature of the lumen or of the supporting elements. At some finite point in each individual the lumen of the trachea divides to form the bronchi, but the precise location of the point of divergence is highly variable. The point of change from one passage to two is not always where the elements cease to be complete rings.

Miller (1934) suggested using the position of the pessulus or the point of insertion of syringeal muscles as reference points for syringeal comparisons. In his study of owl vocal mechanisms he used the pessulus as a base point. For comparisons among the Strigidae the pessulus offers a stable point, but in the suboscine passerines the position of the pessulus does not show clear relationship to muscles and other cartilages. Moreover the presence or absence of the pessulus shows individual variation in at least one species (*Tyrannus tyrannus*).

Throughout the nineteenth century the reference point in syringeal descriptions was the so-called "tracheo-bronchial" junction, the point at which one can say that anterior ("tracheal") elements are complete and posterior ("bronchial") ones divided or double. Difficulty arises in designating as tracheal or bronchial those elements which are incomplete dorsally or ventrally; usually they have been called tracheal.

Some authors have recognized that divided elements are not always uniform. Garrod (1877a) noted the similarity of the anterior divided elements of pittas to the obviously tracheal complete elements. Lowe (1942) suggested that the four flattened "bronchial rings" (A-1 through A-4) of *Manacus vitellinus* might, "in fact, be tracheal derivates." In this case, he concluded, the syrinx of *Manacus* would be "tracheophone." Evolutionarily all divided A-elements may be derived from complete ones, but embryologically they are probably never complete, judging from *Sayornis* and *Fluvicola*. The words "tracheal" and "bronchial," usually associated with the gross configurations of the air passages, do not lend themselves to descriptions of the supporting cartilages, which vary with greater complexity than do the passages.

Designation of the entire syrinx as tracheal or tracheo-bronchial depends on understanding the functions of syringeal components. Assumptions regarding the functions of certain parts of the syrinx sometimes have been made with little evidence. Müller (1847) named the group of birds which possess Membranae tracheales the "Tracheophones," a term used by many subsequent authors. Implicit in the name is the assumption that the Membranae tracheales are the primary source of sound vibrations. Available evidence indiciates that in this type of syrinx, as in most other types, at

least some vibrations are produced by the internal tympaniform membranes (Ruppell, 1933). Members of the furnariid genus *Synallaxis* appear to lack the Membranae tracheales at hatching, yet the nestlings are quite vocal (Dorst, 1963). The sounds of the young are quite different from those of the adults, but the differences may well be due to size effects or to the development of controls, rather than to the use of a different part of the syrinx. If the tympaniform membranes are a source of sound, the ovenbirds and their relatives must be said to have a "tracheo-bronchial" syrinx, as do all other passerines.

In short, it is meaningless to apply positional terms to the syrinx and to use them as taxonomic characters without an understanding of syringeal mechanics, or without carefully defining the structural limits of the syrinx. The use of the adjectives "tracheal" and "tracheo-bronchial," particularly, requires the definition of element types, as well as the criteria for deciding what constitutes the syrinx. The latter question hinges on the role of the internal tympaniform membranes and of the extrinsic muscles.

THE EVOLUTION OF THE SYRINX

THE PRIMITIVE CONDITION.

It is widely accepted that the woodpeckers and allies (Order Piciformes) are the nearest living relatives of the Passeriformes. Similarities in the colic caeca, carotid arteries, leg muscle formulae and certain tendons of the wing were summarized by Garrod (1876). The rollers and allies (Coraciiformes) also are believed to be closely related to the Passeriformes, on the basis of their nude oil gland, heterodactyl foot, and general appearance. In both the Piciformes and the Coraciiformes the syrinx is a slightly modified tracheo-bronchial junction (Beddard, 1898) in which some elements may be fused into a drum and the pessulus is usually, but not always, present. There is only a single narrow lateral muscle, which I have found to be M. tracheolateralis in the few specimens of these orders examined (*Piculus, Colaptes* and *Dendrocopus* in the Piciformes; *Eumomota, Electron* and *Todus* in the Coraciiformes). Beddard referred to "intrinsic" muscles in his descriptions of some piciform and coraciiform syringes, but he described only the insertions, and it appears from his illustrations that this "intrinsic" muscle is M. tracheolateralis in all cases. The only other syringeal muscle in members of these two orders is M. sternotrachealis, which usually inserts in continuity with M. tracheolateralis. This syringeal pattern, with only slight modifications, is found in a large number of avian orders. It is likely that this type of syrinx, widely distributed in modern non-passerines, was present in the stock ancestral to the Passeriformes, Piciformes, and probably Coraciiformes. In the following discussion I will consider it primitive and will refer to it as the "pico-passerine" type. In summary, the characters of the pico-passerine syrinx are: 1) simple tracheobronchial junction, with or without fusion, and without accessory cartilages; 2) pessulus present; 3) intrinsic muscles lacking; 4) M. tracheolateralis narrow and laterally situated; 5) M. sternotrachealis inserting laterally and usually in continuity with M. tracheolateralis.

Among the recent passerines, syringes of the pico-passerine type are found in the Eurylaimidae, Philepittidae, Pittidae, Phytotomidae, and Acanthisittidae, and in some members of the Tyrannidae, Cotingidae and Pipridae. There is no evidence in the present simple syrinx of these birds to show that it did not evolve from a more elaborate one, but one might expect some vestige of the more complex condition to remain. The presence of the drum in the Acanthisittidae suggests that the ancestors of this group might have possessed intrinsic muscles (usually found in association with fusion of lower A-elements), but the drum may have some other function than providing a stable base for the intrinsic muscles.

FUNCTIONAL CONSIDERATIONS.

Any discussion of evolutionary changes is clarified if the direct functional significance of those changes is understood. Unfortunately there is little experimental evi-

dence relating to the mechanics of the syrinx, most theories of syringeal operation being based on anatomy and on acoustic analysis. In one of the few *in vitro* studies to date, Rüppell (1933) showed that in non-passerines the internal tympaniform membranes are the primary source of sound vibrations. Miskimen (1951) demonstrated that the same membranes are also the primary source of sound in the songbirds ("oscines") and that the semilunar membrane is relatively unimportant.

Greenewalt (1968) studied the vocalizations of a number of passerine and non-passerine birds, in the most thorough analysis of the acoustic basis of bird song yet done. He divided vocalizations into two basic "domains," whistled and harmonic. In the former the sound is virtually sinusoidal and nearly all of the amplitude is in the fundamental harmonic. In the latter the syrinx operates below a certain threshhold frequency (the level of which depends on various characteristics of the syrinx), below which the oscillations cease to be sinusoidal. As the operating frequency is lowered, there is a gradual shift in dominant amplitude from the first to the second, then to the third and higher harmonics.

The sound produced in either domain "can be modulated, in either frequency, or in amplitude, or more usually in both, with extraordinary rapidity, so rapidly in fact that human ears cannot perceive the modulations as such, receiving instead an impression of notes of varying quality or timbre" (Greenewalt, 1968, p. 176). The two forms of modulation, amplitude (AM) and frequency (FM), may or may not be related to each other and, if they are related, the relationship may be direct or inverse.

A further phenomenon greatly increases the information potential of an individual bird's song. Borror and Reese (1956) and Thorpe (1961) showed that some birds produce simultaneous and acoustically unrelated frequency patterns, suggesting that the right and left halves of the syrinx operate independently. Greenewalt (1968) demonstrated that this situation is widespread among birds of many orders and that the independence of the two sources is nearly complete. They may operate simultaneously or at different times—often one voice is starting as the other is tapering off—in the same or different domains, and with the same or different AM-FM relationships.

Greenewalt (1968) postulated a mechanism of avian sound production based on earlier work by Setterwall (1901), Rüppell (1933) and Miskimen (1951) and on applications of acoustic theory to current knowledge of syringeal structure and of vocal characteristics. It is generally agreed that the internal tympaniform membranes (ITM) are the primary source of sound vibrations and that their vibrating frequency depends on tension controlled by the syringeal muscles. Greenewalt suggested that this tension is produced by a pressure differential between the interclavicular air sac (surrounding the syrinx) and the lumen of the bronchus. Each ITM is an independent vibrator. With the bronchus prevented from collapsing by the C-shaped elements, the ITM bulges inward, constricting the air passage. Greenewalt also suggested that the passage would be constricted through the tension of the syringeal muscles, but it seems to me that the muscles, if they increase membrane tension, would tend to draw the ITM out of the bronchus, reducing the constriction of the passage. Changes in the shape of the B-elements, induced by the muscles, would probably also alter the degree of constriction of the bronchial passage, but it is difficult to predict how this would affect membrane tension and vocal output.

Chamberlain et al. (1968) manipulated muscles in the excised syrinx of the common crow (*Corvus brachyrhynchos*) and concluded that the primary role of the

intrinsic muscles is to control the positions of A-1 (their B-3) and B-1 (their B-4), the latter rotating around its long axis to increase tension on the external tympaniform membrane (ETM). The passage is constricted by the physical insertion of the anterior edge of B-1 as it rotates inward. The moving air further constricts the passage, by the Bernoulli effect, and sets the membranes, internal and external, into vibration. Chamberlain et al. noted that the ventral end of A-1 has a ventromedial cartilage (the "cartilago tensor" of some earlier authors) that "turns the i.t.m. close to the e.t.m." The muscles acting on A-1 were found to be M. bronchialis anticus, M. bronchialis posticus, and M. bronchotrachealis posticus.

Vibrations of the internal tympaniform membranes thus provide the basic vocal frequency or "carrier frequency" (Stein, 1968). Greenewalt and Stein have both noted that the external tympaniform membranes are too thick for high frequency vibrations. Stein postulated that frequency modulations might arise from a second oscillator in the ETM and external labium. Greenewalt suggested that modulating oscillations might be present in the syringeal muscles themselves.

It is evident from the studies of Miskimen (1951) and Chamberlain et al. (1968) that control of each tympaniform membrane is vested in several muscles and that a single muscle, through complex movements of the element of insertion and through ligamental connections with other elements, may affect more than one element, labium or membrane. The roles of the various parts of the syrinx in producing the complex sounds described by Greenewalt and his many predecessors will be elucidated only by careful *in vivo* and *in vitro* observations of the syrinx in action.

Usually neglected in discussions of syringeal function is the fact that oscine songs are both learned and innate. Andrew (1957), Hinde (1958), Lanyon (1957), and others have demonstrated that adult song is the result of innate factors, reception of songs of other individuals, rehearsal and feedback. The uniformity of syringeal structure among oscines suggests that inherited and acquired patterns in the central nervous system usually play a far greater role in determining the characteristics of song than do patterns of syringeal musculature. I have examined the syringes of individuals of several pairs of sympatric sibling species that rely largely on song for species recognition. The syringes of the eastern and western meadowlarks (*Sturnella magna* and *S. neglecta*) are indistinguishable, yet their songs are strongly different (Lanyon, 1957). The situations in the European warblers *Sylvia borin* and *S. atricapilla* (cf. Thorpe, 1961) and in certain North American flycatchers of the genus *Empidonax* (cf. Stein, 1958) closely parallel that in meadowlarks.

What relationship, if any, exists between the complexity of the syrinx and that of the song? Greenewalt (1968) asserted that certain non-passerines and non-oscine passerines produce songs as complex "as those characteristic of the most accomplished oscines," considering complexity in terms of elaborate modulations. The better songsters among the oscines, he noted, are capable of greater variety in their songs, and in certain species there is a greater individual frequency range than any found in non-oscines. Greenewalt felt that the complex oscine syrinx offers little or no functional advantage over the simple syrinx found in most non-passerines and in certain passerines.

A review of accounts by field observers provides a somewhat different picture, but we must remember that Greenewalt is comparing specific cases, not general trends. Passerines with the pico-passerine type of syrinx produce rather simple calls, most of which can hardly be termed songs, and there is certainly a trend toward longer and more elaborate songs from the broadbills to the oscines. The broadbills (Eurylaimidae),

pittas (Pittidae) and most of the "typical" cotingas (Cotingidae) utter whistled notes or harsh calls, either virtually unmodulated or slowly modulated. Descriptions of the songs or calls of this group vary depending on the listener. The predominant characteristics are the use of short notes repeated rhythmically, or long, steady notes, usually with little change in pitch. Smythies' (1940, p. 289) description of the vocalizations of the broadbill *Psarisomus dalhousiae* is typical of this category: " a not unmusical, rather shrill, loud whistling call of five to eight notes all on the same pitch; a soft churring note when feeding; an occasional single 'weet' call; and several harsh tin-kettley notes when annoyed."

Among the Tyrannidae and Pipridae the spectrum of vocalizations runs from notes as simple as those of the broadbills to songs, as noted above, as complex as those of oscines. In all cases the individual repertoire is limited. The majority of flycatchers and manakins produce relatively simple songs, however, and it is safe to state that, as a group, they are less accomplished than the oscines. A comparison between syringeal and vocal complexity within the Tyrannidae would undoubtedly prove interesting.

In the lyrebirds (*Menura*) and scrub-birds (*Atrichornis*) the use of song is highly developed. The most striking vocal feature of these birds is that most of the vocalizations are imitations of the songs of true songbirds (oscines) and non-passerines. To the human ear the pitch, melody and timbre (overtones) of lyrebird imitations are indistinguishable from the songs on which they are modeled. Individual lyrebirds also learn to imitate mammal calls, mechanical sounds, and even the rustling noise produced by the feathers of cockatoos (Chisholm, 1951). The scrub-birds are second only to the lyrebirds as mimics. I know of no acoustical analysis of lyrebird songs comparable to that done by Thorpe (1959) of mimics of the human voice. Robert C. Stein (personal communication) found the songs of lyrebirds to resemble only superficially the songs on which they are based. Certainly the vocal ability of the Menurae, which have slightly simpler syringes that the oscines, demonstrated the importance of non-syringeal factors in singing "ability."

Taken collectively, the oscines amply deserve the name "songbirds," for they include virtually all of the species commonly associated with elaborate, melodious voices, pleasing to the human ear. Acoustically the group includes an extreme range of vocal abilities. Some, such as the swallows, waxwings, and pipits, are capable of less elaborate or varied songs than are found in many suboscines. In other songbird families, notably the thrushes (Turdidae) and sparrows (Fringillidae), many species are distinguished by elaborate and varied songs and large individual repertoires. Despite the large amount of variation in vocalizations among the various oscine families, the syrinx is of about the same complexity throughout the suborder. In more vocal groups (and sometimes in male individuals) the volume of syringeal musculature is larger than in those groups that sing less and, particularly, that sing less loudly. Evidently the major factor in vocal diversification in the oscines has been changes in the nervous system, rather than in syringeal structure.

REVERSIBILITY AND EVOLUTIONARY TRENDS.

A concept fundamental to the past use of syringeal morphology in passerine taxonomy is that the evolution of the syrinx has proceeded from the simple to the

complex in a smooth series. Garrod, Forbes, and most of their contemporaries seem to have accepted as axiomatic the idea that syringeal evolution has moved in one direction only, toward complexity. The evidence is largely circumstantial. There are no known passerines (and very few nonpasserines) that do not use vocalizations in some aspect of their existence. Selection seems to have favored considerable reliance on vocal communication and functional degeneration of the syrinx would be maladaptive. One can conceive of a population in which vocalizations have lost their biological significance in favor of some other form of communication. Selection in such a population might favor simplification of the tracheobronchial junction, perhaps for respiratory advantages. Selection of this type may have been responsible for the absence of any tracheobronchial specializations in the New World vultures (Cathartidae). The lack of a syrinx in the Cathartidae was first noted by MacGillivray (1838) and has been "discovered" by several authors since then (Wunderlich, 1886; Gadow and Selenka, 1893; Beddard, 1898; Maynard, 1928; Miskimen, 1951).

Perhaps the least vocal of passerine birds are certain of the "arena" species, such as the cocks-of-the-rock (*Rupicola*) and some manakins (*Pipra* and *Manacus*), in which vocal sounds are partly replaced by mechanical ones (Snow, 1962). Eugene Eisenmann informs me that outside their arenas even these manakins are quite vocal. Although largely silent in the dancing arenas, cocks-of-the-rock have several notes used for communication among males (Gilliard, 1962). In the large majority of other passerines the reliance on vocal communication is such that even slight functional impairment of the syrinx would seriously penalize its owner in reproduction.

The extent to which tracheal modifications have gone in a few species suggests that the interference by the syrinx with respiration is not great. Extended coiled trachea are found in several non-passerine groups (swans, cranes, and some sandpipers). One might expect the longer trachea to be disadvantageous in breathing, but apparently the vocal advantages outweigh any respiratory disadvantages. The only passerine birds known to have extended tracheae are the Trumpet Birds (Paradiseidae, *Manucodia*) in which the length of the trachea may be as much as five times the length of the bird without its tail. (Forbes, 1882b). Two specimens of *Manucodia* measured by me had body lengths of about 150mm (from beak to pygostyle) and tracheae 522 and 836 mm long. The trachea forms a flat coil between the skin and the pelvic musculature. A long trachea must greatly increase the amount of residual air in the respiratory system, but it apparently allows the bird to produce a sound of exceptional carrying qualities.

In most passerines the respiratory disadvantages are less obvious, but one might expect that in the absence of continued selection for an elaborate syrinx the tracheobronchial region would revert toward the simpler primitive state. In some oscines of limited vocal abilities, such as swallows and waxwings, the syringeal musculature is very thin, but the same muscles are present as in other oscines. The small size of the internal tympaniform membranes in the bronchi of swallows may be due to a requirement of high pressures in the lungs or in the interclavicular air sac, correlated with their highly aerial existence. The swifts, which may be considered nonpasserine counterparts of the swallows, have well-developed internal tympaniform membranes (Beddard, 1898) despite apparent similarities in respiratory requirements.

I know of only one case in which the present syringeal structure suggests that muscles have been lost. The New Zealand Wrens, *Xenicus* and *Acanthisitta,* possess

a well-developed drum but no intrinsic muscles. In other passerine groups extensive fusion of elements is correlated with well-developed intrinsic musculature. It is possible that the drum in the Acanthisittidae evolved in conjunction with strong syringeal muscles that have since been lost. Published accounts differ concerning the singing abilities of the New Zealand Wrens. Guthrie-Smith (in Oliver, 1955) mentioned "a loud 'cheep' " as the alarm note of *Xenicus longipes*, whose "conversational notes are a faint rasping sound." M'Lean (1911) felt it doubtful that *Acanthisitta chloris* has a real song and mentioned a faint call note "sit" and a rattling alarm note "str-r-r-r." Potts (in Dawson and Cresswell, 1949) mentioned the "twittering song" of this species. Watters (1950) wrote of its "distinctive 'cheep'." Certainly the Acanthisittidae have a limited vocal repertoire compared with other passerines. Unfortunately so little is known of the anatomy of this family that the significance of their unusual syrinx cannot yet be understood.

If we accept the current idea that the oscines are the most highly evolved of passerine birds, it is quickly evident that the trend has been toward greater reliance upon all types of vocal communication. There is some circularity in this conclusion, for syringeal structure and elaborate songs have been a major factor in the current placement of the oscines. Regardless of the evolutionary order, seems to be a general correlation between the intricacy of the syrinx and the complexity and biological importance of song.

The First Pair of Syringeal Muscles.

I have suggested above that the ancestral pico-passerine syrinx lacked intrinsic syringeal muscles. From this condition intrinsic muscles could have evolved either *de novo,* i.e., without a direct relationship to any previously existing muscle, or through the subdivision of one of the extrinsic muscles.

De novo appearance of an intrinsic muscle seems possible, but is difficult to demonstrate. Genetic control over muscle formation has not been studied, but it seems unlikely that a discrete functional muscle would appear through a single mutation. If a mutation should lead to the appearance of a few fibers in a part of the syrinx previously devoid of muscle, and if the new fibers were functionally advantageous, they might provide the basis for the evolution of a new muscle.

The second form of origin of new muscles, through the division of existing ones, appears to be more easily demonstrated. The configuration of extrinsic and intrinsic muscles in some birds may be of aid in identifying the "parent" muscle. This is particularly true in the few cases, discussed below, in which the evolution of the new muscle appears to be incomplete. Of the two extrinsic muscles, M. tracheolateralis seems more likely than M. sternotrachealis to produce an intrinsic muscle. Evolution of an intrinsic muscle from an extrinsic one requires that the latter be in contact with the trachea for part of its length. In most modern birds M. sternotrachealis extends from an origin posterior to the syrinx obliquely to its insertion, with little direct contact with the trachea except in the region of insertion. Derivation of the first intrinsic muscle from this type of M. sternotrachealis would require not only a new subterminal attachment, but also a complex rearrangement of the resultant muscles to attain any known configuration.

The derivation of the first intrinsic muscle from M. tracheolateralis is not only evolutionarily possible, but is sustained by evidence from modern forms. Hypothetically the pattern of this change would be as follows: 1) Primitively, M. tracheolateralis extends down each side of the trachea to insert on a lower A- or B-element. The muscle is loosely attached to the trachea by elastic connective tissue along its entire length. Symmetrical contraction of both Mm. tracheolaterales results in shortening the trachea (unless opposed by the Mm. sternotracheales) and in moving the elements of insertion relative to the adjacent elements. 2) A condition gradually evolves in which the attachment of the muscle to one of the underlying A-elements (A-6, for example) is strengthened. Such an attachment, if accompanied by appropriate innervation, results in more sensitive control over the element at the terminus of the muscle at some sacrifice of distance through which the element may be moved. 3) If favored by selection, the intermediate attachment becomes stronger, resulting in an insertion on A-6 for the anterior portion of the muscle and a new origin for the posterior portion. 4) Ultimately there is complete loss of fiber continuity across the new attachment and the posterior section may be considered a distinct muscle. Although bilateral symmetry is not a requisite of the process described above, it would probably be selectively advantageous, by reducing the distortion of the syrinx during muscle contraction.

The increase in attachment that results in the new muscle might be one of two types: a) Starting with the deep fibers across the full width of M. tracheolateralis, it could involve more and more superficial fibers until the entire thickness of the muscle is attached, or b) starting at one edge with the full thickness of the muscle, it could expand across the muscle until all of the fibers are attached. The end result is the same in the two cases. The new muscle has its dorsal and ventral edges in line with those of the anterior portion (which may still be called M. tracheolateralis); its fiber direction and direction of action are the same as those of the parent muscle; and its insertion is the same as previously.

The present syringeal structure of some members of the Tyranni suggests that both types of derivation from M. tracheolateralis may occur. In the cotinga *Xipholena* and the tyrannids *Myobius* and *Pyrrhomyias* there are no intrinsic muscles, but some deep fibers of M. tracheolateralis are attached to one or two elements of the trachea some distance from the insertion of the muscle. The attachment is weak, involving only connective tissue, without apparent interruption of fiber continuity.

In one specimen of the manakin *Schiffornis turdinus,* the interrelationships of the extrinsic and intrinsic muscles suggest that the latter arose from the former. The well-developed intrinsic muscle is covered by a thin layer of the superficial fibers of M. tracheolateralis. The deeper fibers of the extrinsic muscle insert immediately anterior to the origin of the intrinsic muscle. In *S. virens* and in the other specimen of *S. turdinus,* the intrinsic muscle is nearly identical but is not covered by *M.* tracheolateralis, all of which inserts as do its deeper fibers in the anomatous specimen of *S. turdinus.*

A possible example of the evolution of an intrinsic muscle through the attachment of one edge of M. tracheolateralis is found in the small tyrannid *Tachuris rubrigastra* (Pl. 13). The long, narrow intrinsic muscle, M. obliquus ventralis, is paralleled by a long dorsolateral branch of M. tracheolateralis, while the short ventral fibers of the latter insert immediately anterior to the origin of the intrinsic muscle. This con-

figuration could also have arisen through the complete "cutting off" of the terminal part of M. tracheolateralis, followed by broadening and then elongation of the old muscle into a position adjacent to the new muscle.

Evolutionary shifts in muscle attachments are discussed in a separate section (below).

The use of modern species as examples of intermediate situations should not be inferred to mean that they themselves are ancestral to existing birds with fully evolved intrinsic muscles. The presence of "half-evolved" intrinsic muscles in *Xipholena, Myiobius* and *Pyrrhomyias* may mean that these groups are still evolving intrinsic muscles, or merely that this type of musculature is optimal for producing the types of vocalizations favored in these birds.

In addition to birds possessing a single pair of intrinsic muscles, there are many with balanced dorsal and ventral muscles. Examples of the balanced type include all of the woodcreepers (Dendrocolaptidae) and ovenbirds (Furnariidae), one manakin (*Corapipo*), lyrebirds and scrub-birds (Menurae) and oscines (Passeres). The dorsal and ventral muscles originate on the trachea at the insertion of M. tracheolateralis and insert at the respective ends of certain cartilaginous elements. These intrinsic muscles could have evolved consecutively, but in view of their balanced action, it seems more likely that they appeared simultaneously. If so, their evolution probably involved both the formation of a subterminal attachment and the splitting into two fasciculi at the insertion. Either of these changes could have happened first, or they could have occurred at the same time. The insertions of the fasciculi then shifted to the ends of the elements on which they inserted. In view of differences in the cartilages, it is likely that this process occurred separately in at least three lines of evolution, leading, respectively, to the woodcreepers and ovenbirds, to *Corapipo,* and to the Menurae and oscines.

Additional Intrinsic Muscles.

In addition to the dorsoventrally symmetrical muscle systems just discussed, there are syringeal patterns among the Tyrannidae that involve two pairs of intrinsic muscles. The possible sources of the second muscle are similar to those of the first: *de novo,* from M. tracheolateralis, or from the first intrinsic muscle. The arguments concerning *de novo* appearance are the same as for the first muscle, with as little evidence, and need not be repeated.

In the Olive-sided Flycatcher (*Nuttallornis*) the short lateral intrinsic muscle, M. obliquus lateralis, is isolated from the ventral intrinsic one, M. obliquus ventralis, by an extension of M. tracheolateralis (see Pls. 9 and 10). In *Empidonax, Myiochanes,* and other flycatchers believed to be closely related to *Nuttallornis,* the lateral intrinsic muscle is absent and its place is occupied by the extrinsic muscle. M. obliquus lateralis in *Nuttallornis* could have resulted from a "cutting off" of the lateral terminal region of M. tracheolateralis in the manner postulated above for the evolution of the first intrinsic muscle. M. obliquus lateralis could also have been derived from M. obliquus ventralis prior to the shift of the latter into its present position. This derivation presumes an earlier divergence of *Nuttallornis* from *Empidonax* and *Myiochanes* than is suggested by other features of their anatomy.

In many tyrannids with two pairs of intrinsic muscles, the evidence suggests that the second evolved from the first. In the genus *Elaenia* and its relatives, the second muscle seems to have evolved only recently. The two intrinsic muscles lie closely adjacent, with their insertions continuous and their origins barely separated (not quite separated in one individual of *E. chiriquensis*). The process of change from one muscle to two seems to have involved a gradual increase of the muscle fibers at the two edges of the broad intrinsic muscle and subsequent or contemporaneous loss at the middle. If the two intrinsic muscles provide better modulation than one, it is reasonable to assume that their appearance in the large genus *Elaenia,* with many similar sympatric species, reflects the use of voice in species isolation.

In *Myiarchus,* another large tyrannid genus containing many sympatric species, vocalizations are the most important means of species recognition (Lanyon, 1963). Apparently some populations, and possibly whole species, are in the process of evolving a second intrinsic muscle through a process like that in *Elaenia.* It is doubtful that complete separation of the lateral head of the muscle has taken place. Miskimen (1963) described a discrete lateral muscle, but the degree of separation found was not stated. It would be interesting to compare large numbers of individuals of sympatric *Myiarchus* species with individuals of species whose ranges do not overlap with other *Myiarchus.*

The pattern of evolution of the short muscles in the lyrebirds and oscines appears to have been different from the evolution of M. obliquus lateralis of the Tyrannidae. M. bronchialis posticus is a short deltoid muscle originating along a line that extends from the lateral surface of the drum at about A-5 in a spiral toward the dorsal surface at A-8. The precise position is variable, but usually most of the origin is lateral. In the Mynah, *Gracula religiosa,* the dorsal limit of the origin is continuous with the origin of the longer dorsal muscle, M. bronchotrachealis posticus. The insertions of the two posticus muscles are usually on the same element, A-2, sometimes also on A-3. It is likely that the shorter muscle evolved through a separation of the deep fibers of M. bronchotrachealis posticus together with a posteroventral shift in the origin of these fibers. In their present form the two muscles are very close in the lyrebirds and in many oscines, with the longer muscle partly covering the shorter one.

A fourth intrinsic muscle, M. bronchialis anticus, is found only in oscines. The logical "parent" of this muscle is M. bronchotrachealis anticus, a long muscle that lies superficial to it. M. bronchialis anticus originates on the ventral and lateral surfaces of the drum at the level of A-7 or A-8 and sends a fasciculus on each side of the long muscle; one, pars medialis, inserting on the ventral end of A-2 or A-3, the other, pars lateralis, on the ventral end of A-1. Usually the fasciculi of M. bronchialis anticus are in contact beneath M. bronchotrachealis anticus, but in some families the fasciculi insert separately. The evolution of the short muscle probably involved the same mechanism as suggested above for M. bronchialis posticus.

Changes in Muscle Shape and Attachment.

Changes in the shapes of muscles and shifts in their attachments are important factors in the evolution of syringeal complexity. The "ease" with which modifications can be evolved in a population probably depends on their effect on syringeal operation,

the extent of genetic change needed to produce them, and the importance to the individual of vocal conformity.

The oblique ventral muscle found in most tyrannid flycatchers appears to have evolved from one in which the fibers were anteroposteriorly oriented. In many tyrannids M. obliquus ventralis is a short, broad muscle in which only the ventral fibers are oblique (see, for instance, *Lichenops,* Pl. 7). The oblique ventral fibers apparently confer a vocal advantage over straight ones in certain situations, for frequently the whole muscle is oblique (*Empidonax, Pogonotriccus,* and *Leptopogon* are examples). This condition probably evolved through the gradual increase ventrally of the oblique fibers with the loss of the lateral ones. Sometimes, as in *Empidonax,* the insertion of M. tracheolateralis appears to have moved posteriad into the space beneath the intrinsic muscle. Changes in the type of origin have often followed the shift of M. obliquus ventralis. When its origin is directly on the tracheal elements, the deep fibers must be shorter than the superficial ones. In a short thick muscle, such as that in *Tyrannus,* the deep fibers are only about one-third as long as the superficial ones, a condition that must reduce the mechanical efficiency of the muscle. Greater uniformity of the applied force results if all of the fibers are the same length and this has been approached in some genera (*Empidonax, Elaenia* and others) by the evolution of a midventral tendinous raphe at right angles to the fibers. If the Mm. obliqui ventrales operate simultaneously and are attached to opposite sides of the raphe, the latter has little mechanical function other than to anchor the muscles to the trachea when at rest. In the specimen of *Aphanotriccus* examined the raphe extends only about nine-tenths the width of the muscle. In *Arundinicola* only about two-thirds of the fibers are attached to the raphe, the remainder being continuous between the pair of muscles. In some populations and possibly entire species of *Sayornis* the raphe is wholly lacking, all the superficial fibers being continuous across the midline. The conditions found in *Aphanotriccus* and *Arundinicola* suggest that the raphe was once present in *Sayornis.*

Tendinous insertions are evidently acquired rather easily in some genera. The syrinx is rather uniform in *Elaenia,* but in some species M. obliquus ventralis inserts by a tendon to B-1, in others directly on A-1. In both cases the fibers terminate at A-1, suggesting that the tendon was derived from the A-1/B-1 membrane rather than from the connective tissue of the muscle itself. It would seem a simple step to convert the superficial layer of the tough A-1/B-1 membrane into a broad thin tendon, leaving the deeper layers intact.

Evolution of Cartilaginous Elements.

Evolutionary modifications in syringeal musculature are almost invariably accompanied by changes in the related cartilages. The changes may be limited to the existing cartilages or they may involve the acquisition of new elements. Modifications of the existing cartilages may involve width, thickness, radius of curvature, shape, consistency, and fusion. Most alterations appear to occur as responses to changes in stress, either within the syrinx or from other sources.

In every passerine whose syrinx has been studied, there are some muscles for vocalization in the tracheobronchial region and the cartilages in this region differ from those elsewhere in the trachea and bronchi. The major modification of the

cartilaginous elements in the simplest syrinx is a broadening and thickening of the elements on which muscles insert. The acquisition of broader and thicker muscles is usually associated with expansion and sometimes fusion of those elements whose movement would be detrimental to vocal control. If the syrinx is composed of narrow elements with wide spaces between them, contraction of a muscle parallel to the tracheal axis results in shortening the syrinx along the entire length of the muscle, instead of moving only the element on which it inserts. Either action could be selectively advantageous. Where the muscle axis is entirely parallel to the axis of the syrinx, the force may be restricted to the element of insertion by the elimination of the membranous spaces between elements. In the flycatcher *Pitangus sulphuratus* the lower A-elements are closely fitted together but not fused. In most other cases in which the elements are in close contact with one another there is fusion at a few points.

When the direction of muscle force is not parallel to the syringeal axis, the cartilaginous elements are subjected to shearing and torsion stresses, in addition to compression. The problem is alleviated by the fusion of two or more elements into a drum. The fusion may be incomplete, as in the tyrannids *Pogonotriccus* and *Tolmomyias,* or complete, as in many other tyrannids, some manakins, woodcreepers and ovenbirds, and most, if not all, oscines.

Accessory syringeal cartilages are of two types in the passerines: the Processi vocales of the Furnarioidea and the internal cartilages found in many of the Tyrannoidea. In both cases the evolution of the accessory cartilages has advanced so far that their derivations are obscure.

Processi vocales are found in all members of the Furnarioidea. They vary in form from thin curved plates to thick rather narrow rods. Their position is always lateral and they are usually anchored to the large, non-attenuate lower elements. The Processi might have evolved through one of several means: 1) *de novo,* formation in the membrane surrounding the lower trachea; 2) anteriad extension of one of the lower A-elements; 3) coalescence of the lateral regions of the elements now adjacent to the Processi; 4) formation in the tendon of a syringeal muscle, probably M. tracheolateralis, in a manner similar to the formation of sesamoid bones.

De novo formation may form the basis for the present Processi, but there is little information bearing on this form of origin. The manner in which the internal cartilages blend into the surrounding membranes suggests that the change from thick membranes to thin sheets of cartilage is not a severe one. The Processi vocales could have evolved through the formation of a thin sheet of cartilage in the membrane surrounding the lower trachea.

If the Processi had evolved from anteriad extensions of some lower A-elements, one would not expect to find fusion seams, which are frequently present, where the processi are rigidly attached to the elements. The woodcreeper *Drymornis* is the only example in this study in which the Processi are integral parts of the lower A-elements. *Drymornis* is unique in having both of the elements carrying the Processi divided, resulting in exceptional flexibility in that part of the syrinx.

Coalescence of the lateral regions of several A-elements seems unlikely to have led to the Processi for in many modern species (most Formicariidae and Rhinocryptidae) careful removal of the Processi reveals intact elements underlying them.

The fourth alternative, formation in a tendon, is a very likely means of evolution of the Processi. In many Formicariidae (*Taraba,* for instance) the Processi are little

more than tendinous straps with cartilaginous centers. The edges of the Processi are firmly bound to the surrounding connective tissue, a situation very similar to that of the sesamoid bones of many tendons. This evolutionary pattern supposes that the Mm. tracheolaterales originally inserted on one of the lower A-elements by a tendon or that such a tendon evolved concurrently with the Membranae tracheales. The evolution of a rigid plate in the tendon would provide more direct control over the lower elements, compensating for the flexibility caused by the presence of the Membranae. Of the alternatives suggested above, the "sesamoid" hypothesis seems to me the best supported by the morphology of recent furnarioids.

The internal cartilages lie in the anterior dorsal part of the internal tympaniform membranes in most tyrant flycatchers, a few cotingas (*Attila* and relatives), a New Zealand Wren (*Acanthisitta*) and an asity (*Neodrepanis*). Small ventral cartilages sometimes lie in line with the ventral ends of one of the B-elements, suggesting that they might be remnants of an element that was once double. The position of the internal cartilages relative to the other elements must depend strongly on their acoustic function. The large dorsal internal cartilages have no clear alignment with any elements, although frequently attached to one or more of them. In some tyrannids (*Capsiempis, Leptopogon*) the internal cartilages are very thin at their edges and blend so gradually into the membranes that only histological examination would show where one begins and the other ends. In short the internal cartilages are nearly always more strongly associated with the internal tympaniform membranes than with the supporting elements of the syrinx, with which they sometimes have no connection. It seems likely that the internal cartilages evolved in the membranes, but the exact pattern of their evolution is likely to remain unknown.

Another syringeal component subject to evolutionary change is the pessulus. This midsagittal bar is found in all passerines except the Furnarioidea, most of the Pittidae, many of the Tyrannidae, and the oscine family Alaudidae (larks). When present, the pessulus does not appear to have undergone much elaboration, except in a few isolated cases. The selective pressures affecting the pessulus are difficult to evaluate, for its role in vocalization is unknown. Situated at the junction of the internal tympaniform membranes, it must be instrumental in functional isolation of the right and left halves of the syrinx, preventing tension on one side from affecting the other. Lying in the dorsoventral diameter of the lower end of the syrinx, the pessulus also prevents compression of the drum or other lower elements.

The evolutionary loss of the pessulus in the Furnarioidea may well be correlated with the need for dorsoventral flexibility. Certainly the Membranae tracheales, with the attenuated elements crossing them, result in exceptional flexibility of the syrinx. In no known furnarioid are there modifications for rigidity in this region as are found in some other types of syringes, in which elements are fused. There are occasionally only divided elements posterior to the Membranae. Selection in this group appears to have favored flexibility in the region of bifurcation and the loss of the pessulus is one means of obtaining such flexibility.

In most tyrant flycatchers in which the pessulus has been lost, its position has been nearly occupied by the medial sections of double A-elements e.g., (*Tyrannus, Myiarchus, Inezia*), or by a broad "plug" of soft cartilage (*Sirystes, Xolmis*). The "plug" cannot be considered a derivative of the pessulus for frequently both are present. Some species of flycatchers appear to be evolutionarily losing the pessulus,

there being individuals with, those without, and intermediates. In the intermediate situation the pessulus is a short rod extending only partway from one surface of the syrinx to the other. That this condition exists in a number of morphologically dissimilar syringes belong to tyrannids not usually considered closely related (*Leptotriccus, Blacicus, Legatus*) suggests that the pessulus is being reduced independently in several evolutionary lines. It will be interesting to determine the complete pattern of distribution of the pessulus among individuals and species of *Tyrannus* and others of the family.

In the pittas lacking the pessulus no elements have assumed the position of the pessulus and the internal tympaniform membranes are continuous from one side to the other, meeting in a smooth curve. The simple syringeal musculature, with its force directed parallel to the tracheal axis and its insertion on the lowest of several divided A-elements probably does not exert a dorsoventral stress in the region of bifurcation. The voices of many pittas have been described. *Pitta arcuata* has "a melancholy whistle" (Shelford, *in* Smythies, 1960) and *P. granatina* a whistled "mellow and musical strain" (Adams, *in* Smythies, 1960). According to Smythies (1940) *P. nipalensis* "is said to have a magnificent double whistle" (i.e., two successive notes). From many similar accounts it is evident that the pittas rely on simple songs, frequently of considerable volume. Careful electronic analysis is needed to determine the role of the membranous continuity in their syrinx.

The absence of the pessulus in the larks does not appear to be correlated with reduced singing "ability" for the family has long been famous for their vocal displays. The striking features of the display are the volume and duration of the song and the flight accompanying it. Tucker (in Witherby et al., 1938, p. 181) described the song of the Skylark, *Alauda arvensis,* usually considered the most musical of the Alaudidae, as being "delivered with great spirit and vehemence . . . a loud, clear, shrill warbling, pleasingly modulated, though of limited compass, sustained unbroken up to 3 or occasionally as much as 5 or more, minutes." Larks occupy large territories in open areas and the males sing while rising to a height of several hundred feet above ground.

Phylogeny, Homology and Taxonomic Characters.

As pointed out by Mayr et al. (1953 p. 42), "it is the avowed aim of a modern classification to reflect phylogeny." The evolutionary taxonomist must erect, either in his mind or on paper, a tentative phylogeny for the group under consideration, remaining aware that his phylogeny is an attempt to organize events that really happened. Consideration of passerine phylogeny is made more difficult by the virtual lack of pertinent fossil material and by repeated instances of convergence and parallelism.

In erecting a phylogeny based on a single system of interdependent characters, such as the syrinx, one must admit that some lines of evolution have several alternatives and that others do not lend themselves to phylogenetic interpretation at all. There are several possible evolutionary lines, discussed below, that could have led to the syringeal patterns of the modern lyrebirds and scrub-birds. The determination of which line was the actual one has important bearing on the use of the syrinx in the taxonomy. The syringeal structure of the Eurylaimidae, Pittidae, and Cotingidae is of little use in determining the phylogeny of these groups. On the other hand, within

the superfamily Furnarioidea syringeal morphology indicates a definite phylogeny more likely to have occurred than other alternatives. I have avoided presentation of the usual phylogentic "tree," because such a diagram cannot be adequately drawn from the syringeal evidence. I will discuss the phylogeny of the various passerine suborders from the aspect of syringeal morphology, drawing occasionally on other anatomical data to clarify certain lines of evolution.

EURYLAIMI.

The simple syringeal pattern of the broadbills is not of great phylogenetic significance, beyond indicating that they have not advanced vocally over the pico-passerine ancestor.

FURNARIOIDEA.

This superfamily of the suborder Tyranni has the most clearcut phylogeny, from the syringeal point of view, of any passerine group, but their syrinx suggests nothing about their relation to other groups. The Membranae tracheales were probably nearly or wholly evolved before the group diversified into the wide variety of forms present today. The Membranae are the most uniform feature of the furnarioid syrinx, except for the absence of the pessulus. Apparently the pessulus was lost early in the evolution of this group, for no trace of it has been found in any modern furnarioid. The diversification of syringeal types led to two major stocks. The ovenbird-woodhewer line (Furnariidae and Dendrocolaptidae) evolved a dorsoventrally symmetrical syrinx with two pairs of muscles. The woodhewers evolved more elaborate Processi with projecting horns for the attachment of muscles. It is not clear whether the presence of horns on the Processi in *Geositta* represents an independent appearance from those in the woodhewers.

The other line, which produced the antbirds (Formicariidae) and tapaculos (Rhinocryptidae), contains three basic syringeal types. The simplest of these, found in *Teledromas, Formicarius, Chamaeza, Grallaria,* and *Conopophaga,* is characterized by large Processi and the absence of intrinsic muscles. There is no evidence to suggest that the simplicity found in this group is secondary. Another group is the "typical" antbirds (*Taraba* and similar forms) with small Processi and ventrally originating intrinsic muscles. The third group, the tapaculos (except *Teledromas*), have large Processi with narrow stems and dorsally originating intrinsic muscles. If, as suggested above, the ancestral Processi were of the small "tendinous" type found in most modern antbirds, the evolution of *Formicarius* and similar forms has been away from the typical antbirds and toward the tapaculos. The latter are less advanced than the antbirds in the complexity of syringeal musculature, but seem to have more highly specialized Processi. *Teledromas,* although it has a syrinx nearly identical to that of *Formicarius,* is less divergent from the other tapaculos than *Formicarius* is from the other antbirds.

TYRANNOIDEA.

The New World families included in the superfamily Tyrannoidea include many genera in which the syrinx has advanced little from the hypothetical pico-passerine model. The presence of simple syringes in many cotingas and in some manakins and

tyrant flycatchers suggests that the most recent common ancestor of this varied assemblage lacked intrinsic syringeal muscles and cartilaginous elaborations. It is possible that intrinsic muscles evolved in several different lines within the Tyrannoidea and may be still evolving. The presence of internal cartilages in the absence of intrinsic muscles (in *Terenotriccus* and a few other suboscines) suggests that internal cartilages were acquired independently of intrinsic muscles. The latter could have been evolved and then lost in the line or lines leading to *Terenotriccus* and similar forms, but unless the loss occurred prior to the presumed radiation into *Terenotriccus, Pyrrhomyias, Myiobius* and possibly *Piprites,* one would not except to find such homogeneity in the resulting syringes. It is also possible that *Terenotriccus* and the similar birds diverged from the other tyrannids before the appearance of internal cartilages, and that internal cartilages appeared separately in the two stocks.

It is difficult, if not impossible, to determine how many times intrinsic muscles have evolved in the Tyrannoidea. In some genera, such as *Schiffornis,* the evolution of intrinsic muscles appears to be not yet complete. In others intrinsic muscles are fully evolved, but related genera with structurally similar syringes lack them completely. A pair of genera exhibiting this relationship are the manakins *Pipra* and *Manacus.* In a few flycatchers (*Todirostrum, Spizitornis, Mecocerculus*) the alignment of the intrinsic muscle with the extrinsic M. tracheolateralis suggests a recent evolution of the former.

Although intrinsic muscles may have evolved repeatedly in the Tyrannoidea it seems less likely that repeated conversion to oblique ventral muscles has taken place. A truly oblique M. obliquus ventralis is found only in association with internal cartilages, except in the manakin *Ilicura.* We do not know what functional relationship exists between these two features of the syrinx, nor what selective pressures are exerted by the general body plan of the bird. There is a great deal of variation in the degree of obliquity of the intrinsic muscles, but in a large majority of recognized tyrannids as well as the Sharpbill (*Oxyruncus*) and the "cotingas" *Attila* and *Pachyramphus,* many of the ventral fibers are oblique. Considering the heterogeneity of external anatomy in the Tyrannidae, one might well expect to find a greater variety of syringeal muscles than are present, if the oblique quality of the intrinsic muscle had appeared in many separate stocks.

If the oblique intrinsic muscles were present early in tyrannoid evolution, it is reasonable to suggest that *Attila* and the other members of the *Myiarchus* group and *Oxyruncus* (as well as *Iodopleura* and *Ilicura*?) diverged from the tyrannid line later than the more colorful cotingas (*Cotinga, Pyroderus,* etc.) and the *Terenotriccus* group.

The flycatcher species *Machetornis rixosa* provides a particularly difficult phylogenetic problem. The Mm. sternotracheales strongly resemble those of *Xolmis* and other "ground tyrant" flycatchers, yet *Machetornis* lacks intrinsic muscles. The relationship of the size of M. sternotrachealis to the degree of activity during singing is unknown, but this muscle, connecting the syrinx to the sternum, is more likely than the intrinsic ones to be affected by the activity of the individual. External features support the relationship between *Machetornis* and the ground tyrants. If the relationship is real, *Machetornis* must have lost the intrinsic muscles which are found in the others. Perhaps the loss of the intrinsic muscles is correlated with the evolution of long, straight, non-tapered bronchi in *Machetornis.* As might be expected, the song of

Machetornis is simpler than those of the ground tyrants (Hudson, 1920; Wetmore, 1926).

Solutions to many questions of the phylogeny of the syrinx in the Tyrannoidea will appear only when *in vitro* (and, perhaps, *in vivo*) experimentation has analysed the functional significance of syringeal components. Careful comparisons between vocal performance and syringeal structure are needed to supplement *in vitro* studies.

MENURAE.

The two families of this suborder, the lyrebirds (Menuridae) and scrub-birds (Atrichornithidae) are similar to each other in basic syringeal structure. The two pairs of long muscles are similar to those of the oscines, providing much of the basis for the widely-held theory that the lyrebirds and scrub-birds represent early offshoots of the oscine line. There are several possible phylogenetic patterns.

1) The evolution of the oscine syrinx produced first the long dorsal and ventral muscle pairs, then a short dorsal pair and, fourthly, the short ventral muscles. The common ancestor of *Atrichornis* and *Menura* diverged from the ancestral stock after the third muscle pair had been evolved. By this hypothesis the Menurae would be monophyletic, in the narrowest sense of the word.

2) A second hypothesis states that the common ancestor of *Menura* and *Atrichornis* diverged from the oscine line at a time when the syrinx had less than three pairs of muscles and a third pair of muscles evolved in the scrub-bird-lyrebird line.

3) and 4) Either of the above alternatives could be applied separately to *Menura* and *Atrichornis;* the common ancestor is not a necessary part of the hypotheses and must be considered separately. In their cartilages, both genera are intermediate between the pico-passerine syrinx and the oscine one, there being specialization of the lower A-elements in the direction of "intermediary bars," but no fusion to form a drum.

5) A fifth possible alternative, one which I consider rather unlikely, is that *Menura* and *Atrichornis* had an ancestor or ancestors in the oscines and that their more simple syringes resulted from the loss of a pair of muscles and of fusion. The loss of muscles does not seem probable in birds that rely so strongly on vocalization.

PASSERES ("OSCINES").

The great homogeneity of syringeal structure among nearly 4000 oscine species (for about a quarter of which the syrinx has been examined) strongly suggests a single origin for the group. The only significant deviations from the general pattern are the lack of the pessulus in the larks and the presence of double B-elements in the swallows (*Hirundinidae*). Even in these groups the muscle pattern is the same as in the rest of the suborder. It is probable that the present syringeal structure was fully evolved prior to the radiation of the oscines into their present diversity. The success of this syringeal pattern is evidenced by its retention in widely differing oscine families.

Homology.

Past applications of syringeal morphology to passerine taxonomy have been based on the assumption, supported by the investigations of Müller (1847) and Garrod

(1873, 1876), that the syrinx is a conservative structure, i.e., that it has changed slowly during the radiation of the ancestral passerine stock (or stocks) into the diverse body plans now found. One purpose of this study is to evaluate the degree of conservatism in the syrinx, in order to determine which aspects of syringeal structure have taxonomic usefulness.

The degree of diversity in the syrinx is clearly not directly correlated with the external diversity of passerines generally. Members of the suborder Passeres are so uniform in syringeal structure that a noticeable departure from the norm has usually been considered strong evidence of phylogenetic separation. The very homogeneity of the syrinx among the oscines, while enhancing its value as a character for subordinal definition, reduces its applicability at the lower taxonomic levels. Several groups of genera, at roughly the family level, exhibit minor but apparently consistent myological variations that appear useful in establishing relationships. Detailed description of these variations is beyond the scope of this work and more specimens must be examined before taxonomic conclusions may be drawn.

In the suborder Tyranni the rate of change in the syrinx, in relation to changes in the whole bird, has evidently been more rapid than in the Passeres. This conclusion is based on the relative diversity of modern forms. The diversity of the syrinx makes it more useful at the lower taxonomic levels than at corresponding levels in the oscines, wherever consistent similarities and differences among structural groups can be recognized.

Consideration of any feature in a phylogenetically based taxonomy hinges on whether or not the feature is homologous in all members of the group under consideration (Mayr et al., 1953; Simpson, 1961). The term "homology" is employed here in the sense used by Simpson (1961, p. 78) meaning "resemblance due to common ancestry," which I interpret to mean that the feature in question was present in the common ancestor. Bock (1963, p. 283) defined homology in terms of descent from "the same feature in a group possessing a high degree of evolutionary homodynamy." The latter term is "the ability with which the same feature may originate and evolve several independent times within a group of organisms." Bock pointed out that the acceptance of this definition leads to the use of broadly based taxonomic groups, as suggested by Simpson (1961, p. 124). I agree with Reed (1960) that the use of Simpson's broad definition of monophyly leads to a classification that is both vertical and horizontal. Such a classification obscures the attempt to describe real phylogenetic events. In the case of passerine birds, it is unlikely that the fossil record will ever assist us in deciding phylogenetic questions, but I cannot agree with Bock that "pseudohomologous" (basically "parallel") features can never be uncovered without either intermediate or ancestral forms. He has pointed out that such features have their basis in the "genetical-developmental potential", and perhaps this potential, if we could evaluate it, would be useful in determining the phylogeny. Understanding the adaptive significance of a structure aids in the analysis. Examples of known "pseudohomology" cited by Bock were uncovered without the aid of fossil forms and frequently (as in the case of the Madagascar "nuthatch" *Hypositta*) without any intermediate forms. The finch-billed lark (*Rhamphocorys*) would certainly be considered phylogenetically allied to the buntings, were it not for the several alaudine features (including the syrinx) that make it clearly a lark. The probability of uncovering non-homologous features increases as a particular adaptive complex is studied in

greater detail and in a greater variety of animals, and as a larger number of adaptive complexes is available for comparison. This should allow one to determine the homology or non-homology of a feature in the narrower sense. If one wishes to employ the narrower concept of monophyly, one must use a narrow definition of homology.

Applied to syringeal morphology, the above considerations underline the handicap imposed by our lack of knowledge of syringeal mechanics. The strictly morphological approach bears fruit, however, when several features of the syrinx can be compared in considerable detail. I am not prepared to state, at this point in our knowledge, that intrinsic syringeal muscles have arisen only once in the Tyrannoidea, nor that conversion to oblique muscles occurred only once. It is possible that the underlying cartilaginous structure of the primitive tyrannoid syrinx was such as to limit the possible muscle configurations. In that event, the repeated evolution of a particular pattern of musculature might be expected wherever selection favored the appropriate vocal pattern. Until more is known about the degree of functional interdependence of the various parts of the syrinx, we can only rely on morphological analyses in drawing inferences about homology.

At lower taxonomic levels, homology of muscle shape or of cartilaginous element configurations is frequently supported by the detailed duplication of a character in several genera. It is at the intergeneric level that homologies are the easiest to demonstrate, through the multiplicity of character details within the syrinx.

The application of syringeal morphology in the Tyrannoidea increases in reliability toward the generic level. At the higher levels relationships are suggested by syringeal similarity, but not as much weight should be attached to the general similarities as may be attached to the more detailed similarities that frequently exist among groups of genera.

For example, nine genera of flycatchers that I term the "*Tyrannus* group" have in common seven myological and cartilaginous features, several of which seem to be so minor as to have only slight functional significance. It is hard to imagine how similarity in such detail could have arisen independently in two lines, starting with a more generalized syrinx. The nine genera of the *Tyrannus* group have external similarities that have caused "skin taxonomists" to consider them closely allied, but even if the nine were externally diverse, homology of the syrinx would remain a strong probability.

A second case, less strongly supported by external morphology, concerns the flycatcher genus *Myiarchus* and several "cotingas" of which *Attila* is an example. The structural agreement is as close as among the *Tyrannus* group, but there are fewer details of similarity. The case for syringeal homology in the *Myiarchus-Attila* relationship rests on muscle shape, element configuration and the shape and number of internal cartilages. The only external character which argues against the *Myiarchus-Attila* syringeal homology is the scutellation of the tarsus, a character now known to be highly plastic.

Taxonomic Applications.

In short, no single feature of the syrinx is taxonomically useful throughout the Passeriformes and different structural characters are valid at the various taxonomic levels. The major characters enumerated below are functionally interrelated to varying

and usually unknown degrees. Their ultimate evaluation must lie in the comparison with the non-syringeal characters, together with which they form the basis for the prevailing classification of the order.

1) Gross anatomical features (major modifications involving most of the tracheobronchial region) are limited to the presence of the Membranae tracheales and Processi vocales in the Furnarioidea. In the remainder of the order the differences are more localized and less profound.

2) The absence of the pessulus is a definitive character for the superfamily Furnarioidea and for the oscine family Alaudidae, but in the Tyrannoidea its configuration is highly variable, even within certain species. Further study may prove it to be of use in some subgroups of the tyrant flycatchers, but at best its taxonomic value will be limited.

3) The degree of fusion of syringeal elements must be applied cautiously as a taxonomic character, for it is evidently related to the type and size of the intrinsic muscles. Fusion and muscle patterns are general indicators of the role of voice in the overall biology of a group and probably are related to some external features. In certain cases, such as in the manakin genera *Manacus* and *Pipra,* peculiarities of fusion are probably indicative of phylogenetic relationships.

4) The internal cartilages of the Tyrannidae and a few others appear to be reliable indicators of relationships at the intergeneric level. Their applicability rests on the wide variety found in the flycatchers, their intrageneric uniformity, and their lack of an obvious functional relationship to other syringeal features. While the internal cartilages may be functionally related to other cartilages and to the muscles, the relationship does not appear to restrict the shape of the internal cartilages, which perhaps exert an independent effect on the voice. The internal cartilages have greater taxonomic validity where they have complex shapes, for the morphological groups are more homogeneous and more clearly separable from each other. Knowledge of the acoustic function of these cartilages will greatly aid in evaluating them as a taxonomic character.

5) Minor peculiarities of the cartilaginous elements are among the most useful characters, because they are probably not greatly dependent upon other characters. Such peculiarities include sharp corners on some A-elements (*Tyrannus*), the dorsally extended pessulus (*Colopteryx*), and even extra elements (*Onychorhynchus, Pitta*). Taxonomic application of any of these peculiarities requires the examination of enough individuals to insure that the "character" is not merely an individual variant.

6) The number of intrinsic muscles has classically been a major character in defining the suborders Menurae and Passeres (Müller, 1847; Garrod, 1876; nearly all subsequent authors) and here it appears to be valid. In the Furnarioidea, the number of intrinsic muscles is useful at the family level. The Eurylaimidae and some families of the Tyrannoidea may be defined as lacking intrinsic muscles, but in the manakins and tyrant flycatchers the character is applicable only at low levels. Two genera of tyrant flycatchers that appear from other syringeal and non-syringeal characters to be closely related may differ in the number of intrinsic muscles (viz. *Elaenia* and *Tyrannulus*). The number of muscles is closely related to the overall shape of the total complex of syringeal muscles. The shape and attachments of each muscle must be examined individually and in respect to other muscles before taxonomic conclusions can be based on the number of muscles.

7) Myological details such as the types and positions of muscle origins and insertions and the shapes of muscles are of rather varied applicability throughout the order. The suborder Passeres may be defined as "acromyodean" (Garrod, 1876) in a general sense, but the opposite term, "mesomyodean," is inappropriate for the rest of the order, in which all intermediates from terminal to middle attachments are found. Specializations of shape or attachment, such as the short, thick intrinsic muscles of *Tyrannus* and some similar species, or the ventral layering of the muscles in *Colopteryx,* seem most likely to show phylogenetic relationships. Certain other myological features, such as the origin of M. obliquus ventralis on a median raphe, are consistent among several tyrannine groups, but are too widespread for use in delimiting a group without overriding other syringeal features.

The results of this study confirm the belief of Müller and many subsequent authors that the syrinx is of value in subdividing the Passeriformes. An exception is its application to the definition of the suborder Tyranni. The superfamily Furnarioidea is based on the uniform distribution of several syringeal features, but the Tyrannoidea cannot be defined on the basis of the syrinx. Certain syringeal characters in both muscles and cartilages appear to be useful at about the family and subfamily levels in the New World Tyrannoidea.

SYSTEMATIC CONCLUSIONS

Taken in conjunction with other anatomical characters, syringeal morphology suggests that the Passeriformes be divided into five suborders: Eurylaimi, Furnarii, Tyranni, Menurae, and Passeres (Oscines).

EURYLAIMI.

Eurylaimidae. The broadbills have traditionally been separated from all other passerines on the basis of their plantar vinculum, first noted by Sundevall 1872 and emphasized by Garrod (1877a), and non-bifurcate spina sternalis. Although the simple syringeal structure supports the belief that the Eurylaimidae are primitive, relative to other passerines, it is of little help in understanding their relationships. They have evolved bright plumage in place of the extensive use of vocalizations for species recognition and courtship. In general their calls are monotonic and simple, produced by a syrinx lacking intrinsic muscles and cartilaginous specialization. The green broadbills (*Calyptomena*) possess elaborations of the anterior edge of the internal tympaniform membrane, and of the Mm. sternotracheales, that set them apart from the rest of the family. These differences support their separation as the subfamily Calyptomeninae.

Philepittidae. The syringeal structure of both *Philepitta* and *Neodrepanis* is remarkably like that of the broadbills *Smithornis* and *Psarisomus* (see Pls. 2 and 17), even to minute details of the cartilaginous elements, but the whole organ is relatively unspecialized. Although the plantar vinculum is absent in *Philepitta,* the spina sternalis is non-bifurcate and pterylosis is similar to that of the Eurylaimidae (Forbes, 1881). Whatever their affinities, the Philepittidae appear to have retained a primitive syrinx while most other passerines have evolved some modifications for song.

FURNARII.

The families grouped by most modern systematists in the superfamily Furnarioidea share an elaborate syringeal form not found elsewhere. No structures even remotely resembling the Membrana trachealis and Processus vocalis are found in other passerines. Aside from zoogeographic considerations, there are no characters to ally them particularly to the Tyranni. Pycraft (in Ridgway, 1907) believed that the distinctions of the syrinx were sufficient to justify subordinal status for the Furnarii and I am inclined to agree with him, when other characters are considered. On the basis

of syringeal structure and other characters (pterylosis, cranial and sternal osteology) the following four families can be recognized.

Dendrocolaptidae. The syrinx of the woodcreepers is distinguished from those of other members of this suborder in possessing prominent dorsal and ventral horns on the Processi vocales. Only this family and the Furnariidae possess two pairs of intrinsic syringeal muscles. The presence of horns on the Processi of *Geositta* could be taken to indicate that *Geositta* is more closely allied to the woodcreepers than to the ovenbirds (Furnariidae), but it appears to be a fairly typical ovenbird in other respects. It is possible that the need for greater mechanical advantage for the syringeal muscles has caused the evolution of horns in the syrinx of *Geositta*, independently of the Dendrocolaptidae, but in this case one would expect to find horns on the Processi of other ovenbirds, which must have been subjected to similar selective pressures.

Furnariidae. The close relationship of this group to the woodcreepers is indicated by the similarity of syringeal musculature, which sets the two families apart from the antbirds (Formicariidae) and tapaculos (Rhinocryptidae). The ovenbirds appear to be separable from the woodcreepers on the basis of the absence of horns on the Processi vocales (except in *Geositta*) and by the possession of schizorhinal nares (Garrod, 1877a).

Formicariidae. The antbirds may be divided into two groups on the basis of syringeal morphology. The majority of the genera examined, to which I apply the term "typical antbirds," are distinguished by having one pair of intrinsic syringeal muscles, a very small Processus, and M. sternotrachealis bifurcate near its insertion. Examples of this group are *Taraba, Dysithamnus, Thamnophilus,* and *Myrmotherula*. The second group, the "ground antbirds," is characterized by the absence of intrinsic syringeal muscles, a large Processus, and a simple M. sternotrachealis. To this group belong *Grallaria, Chamaeza, Formicarius,* and *Conopophaga*. Long-legged terrestrial birds, they appear to be intermediate between the Formicariidae and the Rhinocryptidae. Such intermediacy is suggested by the presence of a four-notch metasternum, classically a rhinocryptid character, in some species of *Grallaria* and in *Pittasoma* (Heimerdinger and Ames, 1967).

Rhinocryptidae. The tapaculos are usually considered separable from the antbirds by the possession of two pairs of sternal notches, but Heimerdinger and Ames (1967) have shown that this character also occurs in the antbirds *Grallaria* and *Pittasoma*. In their syrinx the rhinocryptids possess a simple M. sternotrachealis and a dorsally originating intrinsic muscle. One genus, *Teledromas,* lacks the intrinsic muscle, its syrinx being much like those of *Formicarius* and *Grallaria*. The tapaculos are outwardly similar to the short-tailed, long-legged, ground-living antbirds which they resemble in syringeal structure, but from which they differ in pterylosis (Ames et al., 1968). Only an extensive study of the anatomy, behavior, and other characters of these two groups will determine whether the present family boundaries are natural or artificial.

TYRANNI.

This suborder should probably be restricted to the five New World families of Wetmore's (1960) superfamily Tyrannoidea: Cotingidae, Phytotomidae, Pipridae, Tyrannidae, and Oxyruncidae. The Pittidae can only be judged "incertae sedis" on the basis of our present knowledge. Their simple syringeal structure reflects their use of bright colors rather than vocalizations in species recognition. This syringeal pattern, characterized by the absence of intrinsic musculature and of cartilaginous modifications, does little to suggest the affinities of the pittas. The absence of the pessulus in most pittas probably represents a specialization and cannot be taken as a definite indication of relationship to other forms that lack the pessulus. The pessulus, probably present in the ancestral "proto-passerine" stock, has been lost by several other groups in the order (all the Furnarii, some individuals and species of Tyrannidae, and all of the oscine family Alaudidae), apparently independently. The Pittidae share with the Acanthisittidae the character of bilaminate planta tarsi, but the tendency toward fusion of tarsal scutes is characteristic of long-legged terrestrial birds. The New Zealand "wrens," consisting of the genera *Xenicus* and *Acanthisitta*, were placed by Forbes (1882a) in the "Oligomyodae" (the Tyrannoidea of later writers) solely on the basis of the insertion of the syringeal muscles. The syrinx shows a unique combination of cartilaginous fusion and lack of intrinsic musculature. These two peculiar genera show no clear relationship to any New World tyrannoid group. Without knowledge of other anatomical and behavioral features, it is unlikely that the true position of the Acanthisittidae can be determined. The patterns of egg-white proteins (Sibley, 1970) support the conclusion that neither the Pittidae nor the Acanthisittidae are closely related to the New World Tyrannoidea.

COTINGIDAE.

The cotingas, as treated by Ridgway, Hellmayr, and most modern systematists, contain two distinct groups with respect to syringeal morphology. The majority of genera, which I have retained in the family as discussed low, lack intrinsic syringeal muscles (except for the bellbirds) and internal cartilages. Most rely on structural and chromatic elaborations of the feathers for species recognition and courtship. The remaining genera, consisting of *Attila, Casiornis, Laniocera, Rhytipterna* and *Iodopleura*, possess oblique ventral intrinsic muscles and internal cartilages, thus resembling the Tyrannidae far more than the typical cotingas. The resemblance to the Tyrannidae is further enhanced by their bill shape, strong rictal bristles, and plain coloration (except for *Iodopleura*). The first four genera are discussed under the Tyrannidae.

The members of the *cotinga* group are medium-sized birds, many strongly colored. Their syrinx is characterized by a small amount of specialization of the lower A-elements and only a slight flare at the region of bifurcation. They possess only a narrow M. tracheolateralis in the syringeal region. In this category are the genera

Cotinga, Xipholena, Heliochera, Euchlornis, and possibly *Tityra.* The last of these genera is often separated as a subfamily, for its members have a number of structural peculiarities, such as the bare facial areas and hooked bills, and unusual behavioral traits, such as their habit of nesting in holes.

In the *Pyroderus* group, sometimes called fruit crows, the lower three to five A-elements are enlarged, divided, and usually individually broadened, overlapping like shingles and creating a broad cavity in the region of bifurcation. By contrast, the B-elements are reduced both in number and in size, resulting in rapidly tapering bronchi of short length. In some of this group the anterior portion of the trachea is enlarged to form a long cavity (*Perissocephalus, Cephalopterus*). The fruit crows are the largest of the cotingas, reaching the size of the true crows (*Corvus*). Their colors are more subdued than those of the *Cotinga* group, many being predominantly black. The group includes the genera *Pyroderus, Perissocephalus, Gymnoderus, Conioptilon, Gymnocephalus,* and *Cephalopterus.*

The *Querula* group differs only slightly from the last in syringeal structure. The lower A-elements are more strongly arched, creating a more hemispherical cavity. There is no enlargement of the anterior trachea. The simple musculature of the previous two groups is found here also. In this group are *Querula* and *Carpodectes.*

The four species of bellbirds (*Procnias*) have evolved simple, loud, ringing calls, produced by a highly muscular syrinx. The syringeal cartilages and muscles are so specialized that they tell us little about the relationships of *Procnias.*

The cocks-of-the-rock (*Rupicola*) are sometimes given family status, on the basis of their arena courtship behavior and several structural features. The latter include the crest-like frontal feathers (a feature also found in *Phoenicircus*), syndactyly, and homeomery (the dominant artery of the thigh is the sciatic; cf. Garrod, 1876). The presence of syndactyly may be linked to the courtship behavior, for syndactyly occurs in several unrelated birds that utilize vertical perches, as do the cocks-of-the-rock. The simple syrinx of *Rupicola* is much like that of the typical cotingas, representing little adaptation for elaborate vocalizations.

The cotinga genus *Iodopleura* would appear from syringeal structure to be allied to the Tyrannidae, but differs in coloration and beak shape from other members of that family. Determination of the relationships of *Iodopleura* must await the study of other taxonomic characters.

PHYTOTOMIDAE.

The plant-cutters of the genus *Phytotoma* are said to be closely related to the cotingas on account of the simplicity of their syrinx and their tarsal envelope. Certainly there is no other New World group with which the Phytotomidae agree more closely in these two characters. The evident similarity of the syrinx of *Phytotoma* to that of some cotingas (particularly *Heliochera*) may indicate merely that both groups have retained the primitive syringeal structure, as appears to have been the case with the Eurylaimidae and Pittidae. A complete examination of structural and behavioral characters is needed before the systematic position of the Phytotomidae can be determined.

PIPRIDAE.

A close relationship of manakins and cotingas is accepted by most modern systematists, some of whom question whether the two families are really separable. A reliable means of separating the two groups from the Tyrannidae has long been sought. Garrod (1876) used the arteries of the thigh to separate the Pipridae and Cotingidae (except *Rupicola*) from the Tyrannidae. Ridgway (1907) relied strongly on the form of the tarsal envelope and the degree of syndactyly. Hellmayr (1927) reversed many of Ridgway's decisions, using bill shape and wing modifications as accessory criteria. Although too few manakins were available for a complete analysis of syringeal structure, it is evident from the examination of seven genera that considerable variation exists.

Pipra and *Manacus* are very similar in cartilaginous elements, but differ in musculature, *Pipra* possessing intrinsic muscles, *Manacus* none. *Chiroxiphia* shows relationships to *Pipra* in the cartilages and in the general type of intrinsic muscles. *Corapipo* has a peculiar form of musculature, which Garrod might have called "acromyodean," in that the muscles insert on the ends of the elements. The pattern of musculature, however, is quite unlike that of the oscines and the cartilages of *Corapipo* are not greatly different from those of others of the Tyranni. The cartilaginous structure of the syrinx in *Piprites* is reminescent of that in the small tyrannids *Myiobius* and *Terenotriccus,* while the musculature differs only in being narrower. Except for the *Piprites-Myiobius* complex and *Ilicura,* the few manakins examined show little syringeal similarity to the typical members of either the Tyrannidae or Cotingidae.

The thrush-like manakin (*Schiffornis*) differs from other manakins in that its intrinsic musculature is lateral and slightly oblique. The general appearance of its syrinx, with rather simple cartilages and long, straight bronchi, is quite like that of the cotinga *Lipaugus,* but my specimen of the latter is too badly shot damaged to allow close comparison with either *Schiffornis* or the typical cotingas. *Schiffornis* is unique among the manakins that I have studied in possessing internal cartilages, but the manakins are so heterogeneous in syringeal structure that I have come to expect almost anything.

The military manakin (*Ilicura*), with oblique intrinsic muscles and no fusion of A-elements, stands somewhat apart from the "nucleus" of manakins represented by *Pipra, Manacus* and *Chiroxiphia.* It is no more divergent from this nucleus than *Corapipo, Piprites* and *Schiffornis,* however—all have diverged in different ways—, and only further study will reveal whether or not the tyrannid nature of the syrinx is indicative of the relationships of *Ilicura.*

TYRANNIDAE.

The tyrant flycatchers are the most diverse of suboscine families. Although the "typical" tyrannid could be described as a small olive bird with a flat, slightly hooked

bill and strong rictal bristles, there are more atypical forms than typical ones. Usually the tarsus is exaspidean and the toes lack syndactyly (Sclater, 1888). In all of their external characters the Tyrannidae are so variable that taxonomic boundaries and relationships within the family and with other families are often difficult to determine.

With few exceptions the tyrannid syrinx is characterized by the presence of an intrinsic muscle, M. obliquus ventralis, and internal cartilages. Rarely, a second intrinsic muscle, M. obliquus lateralis, is present. Outside the traditional limits of the Tyrannidae (as revised by Hellmayr, 1927) M. obliquus ventralis and internal cartilages occur in New World Tyranni, separately or together, only in *Oxyruncus, Corythopis,* the manakin *Ilicura* and a few members of the Cotingidae. The Sharpbill, *Oxyruncus,* has a few distinctive structural features and appears to merit family status. *Corythopis* and the "cotingas" are discussed below in the revised family Tyrannidae.

Among the 86 genera of tyrant flycatchers examined in this study, several structural groups may be distinguished, each with a high degree of syringeal homogeneity and with certain features not found elsewhere in the family. Some groups represent variations of a generalized tyrannid form; others are so specialized as to hide their relationships. The remaining genera have either highly specialized or intermediate syringes, making taxonomic placement difficult. The groups below are not presented as subfamilies, for the descriptions do not include all of the characters on which subfamilies should be based. I have attempted to group together genera which syringeal morphology suggests are most closely related. For ease of reference I am handling each group under the name of a typical genus.

1. The *Fluvicola* group is characterized by: the presence of a dorsal cartilaginous plug, to which the short, usually triangular internal cartilages are attached; extreme development of M. sternotrachealis, which usually inserts with three fasciculi; a short, broad, rather flat M. obliquus ventralis, which inserts on A-1. The nucleus of this group are the genera *Xolmis, Neoxolmis, Agriornis, Muscisaxicola, Fluvicola, Gubernetes, Knipolegus, Muscipipra,* and *Phaeotriccus.*

Lichenops [= *Hymenops*] is probably an offshoot of this group, having evolved a much more robust M. obliquus ventralis and associated cartilages. *Satrapa* and *Entotriccus* probably also belong here, differing from the more typical genera in the form of M. sternotrachealis and in the shape of the internal cartilages. *Lessonia,* which differs from the others of the group in the peculiar dorsal pattern of the A-elements, agrees with them in the musculature.

Although all of the above genera were placed by Hellmayr and his immediate predecessors in the subfamily Fluvicolinae, some genera placed in that subfamily do not appear, from their syringeal structure, to belong near the nucleus of the group. The genera *Ochthoeca* and *Colonia* are similar to each other in several aspects of their syringeal morphology and different from the typical members of the *Fluvicola* group. The phoebes (*Sayornis*) agree more closely in cartilages and musculature, as well as in their external appearance, with members of the *Nuttallornis* group. The Vermillion Flycatcher, *Pyrocephalus,* is strongly unlike the typical members of this group in syringeal musculature, but like them in the cartilages. Müller (1847) noted the similarity of the syringeal musculature of this genus to that of the becards (*Pachyramphus*), but in view of the dissimilarities of the cartilages, I believe the myology to be convergent. I do not feel that the syrinx is of much help in determining the position of *Pyrocephalus.*

Machetornis is unlike the *Fluvicola* group in all aspects of its syringeal structure except the form of M. sternotrachealis. It is possible that the great development of this muscle is in some way linked to a strongly terrestrial existence, in which case a strong M. sternotrachealis would be expected to exist in many unrelated long-legged birds. It is true that very robust Mm. sternotracheales are found in the ground-living antbirds, *Conopophaga, Formicarius,* and *Grallaria,* but the mode of insertion of this muscle in the typical antbirds (see *Taraba,* Pl. 3), is more like that of this group of flycatchers. It is not possible to say whether the lack of intrinsic musculature in *Machetornis* is the result of secondary change from a syrinx like that of *Xolmis,* or whether the thick, diffusely attached M. sternotrachealis is convergent, because we do not yet know the functional significance of the various syringeal types.

2. The *Tyrannus* group is syringeally the most homogeneous of the subdivisions. The syrinx is characterized by: close-fitting lower A-elements, usually with ventral fusion; one or more double A-elements, with sharp dorsomedial corners; ventral terminal fusion of two B-elements; short, straight internal cartilages; M. sternotrachealis with diffuse insertion (as in the *Fluvicola* group); short, broad, prominently bulging Mm. obliqui ventrales, which usually do not touch each other at the ventral midline. Of the genera examined in this study, the group includes: *Tyrannus, Muscivora, Tolmarchus, Tyrannopsis, Empidonomus, Myiodynastes, Megarhynchus, Conopias,* and *Pitangus* (*sulphuratus* only). *Pitangus* has some cartilaginous modifications which set it apart from the more typical members of the group. *Pitangus lictor* lacks most of the features of the group and, in view of the structural homogeneity found among those listed above, it is difficult to believe *lictor* and *sulphuratus* are more closely related to each other than the latter is to *Tyrannus* and others with which it shares many syringeal features.

All of the above genera were included by Hellmayr (1927) in the subfamily Tyranninae, but interspersed among them were *Legatus, Sirystes,* and *Coryphotriccus.* I have not examined the last of these, but the other two do not appear to belong in the middle of the *Tyrannus* group in a linear arrangement, since they lack almost all of the syringeal features listed above. *Legatus* seems to be most like *Myiozetetes* in syringeal musculature, but the two are different in several aspects of the cartilages. The syrinx does not indicate much about their position within the family. The systematic position of *Sirystes* has always been uncertain. Ridgway (1907, p. 339) placed it in the Cotingidae, primarily on the basis of its holaspidean tarsus. Hellmayr (1927) placed it in the Tyrannidae without comment, a course followed by most recent authors. The syrinx of *Sirystes* is typically tyrannid in cartilages and musculature with little similarity to the simple syringes of the Cotingidae as restricted above, but its syrinx resembles those of the *Fluvicola* group more than those of the *Tyrannus* group and bears little resemblance to those of the becards (*Pachyramphus*).

3. The *Nuttallornis* group is closest to the *Fluvicola* group in syringeal structure. The most characteristic feature of the syrinx is complete or partial continuity between the Mm. obliqui ventrales. This condition reaches the extreme in *Sayornis,* in which the superficial muscle layer of some specimens is wholly continuous, having essentially two insertions and no origin. In those genera lacking fiber continuity across the ventral midline, the Mm. obliqui ventrales originate on a median raphe, not, as in the *Fluvicola* and *Tyrannus* groups, directly on the ventral surfaces of the cartilages. In

most members of the *Nuttallornis* group M. tracheolateralis extends beneath the oblique muscle to insert on A-1 or A-2. The group includes *Nuttallornis, Sayornis, Myiochanes* [= *Contopus*], *Blacicus, Empidonax, Aechmolophus, Aphanotriccus,* and possibly *Muscigralla.*

The last genus deserves special comment, for some authors have considered it out of place in the Tyrannidae. *Muscigralla* is a very unlikely tyrannid, but its syrinx strongly supports its inclusion in the family. Ridgway (1907, p. 339), noting its holaspidean tarsi, felt that it "probably belongs in the Formicariidae," despite the fact that by his own definition the Formicariidae have taxaspidean tarsi. Hellmayr (1927) included *Muscigralla* in the Tyrannidae, but called it "a bird of doubtful affinities," which "probably belongs in another family." The lack of "tracheophone" features in the syrinx excludes *Muscigralla* from the Furnarii, while the presence of M. obliquus ventralis and internal cartilages supports its inclusion in the Tyrannidae. I have placed it near the *Nuttallornis* group because the musculature of the syrinx agrees closely with that of other members of the group.

4. The *Myiobius* group consists of four genera placed by Hellmayr (1927) in the subfamily Myiarchinae with all of the *Nuttallornis* group. Characteristic of the syringes of this group, which includes *Myiobius, Terenotriccus, Pyrrhomyias* and *Onychorhynchus,* are the possession of two double A-elements and the absence of intrinsic muscles. The four genera seem to be more closely related to each other than to the *Nuttallornis* group, which appears from external characters to contain their closest relatives. The manakin *Piprites* probably also belongs here.

5. The *Myiarchus* group contains some genera placed by Hellmayr (1927) and most other authors in the Cotingidae. The group includes *Myiarchus, Eribates, Attila, Casiornis, Laniocera,* and *Rhytipterna.* In all of these the syrinx is characterized by broad ventral Mm. tracheolaterales with little or no midventral space between the pair; narrow Mm. sternotracheales; the Mm. obliqui ventrales attached directly (without a raphe) midventrally and on one or more A-elements laterally; narrow J- or ɹ-shaped dorsal internal cartilages; a smaller ventral pair of internal cartilages. Several of these features occur elsewhere in the Tyrannidae, but only the above genera are known to possess all of them.

The transfer of *Attila* to the Tyrannidae has been suggested by several authorities. Ridgway (1907, p. 770), while retaining *Attila* in the Cotingidae, noted that, along with *Lipaugus, Casiornis, Sirystes,* and *Tolmarchus, Attila* was "essentially if not typically taxaspidean," differing from the majority of cotingas. Hellmayr (1927) remarked that *Attila* "should probably be included among the Tyrannidae." He felt that "in spite of its exaspidean tarsus and cohesion of the toes," *Laniocera* belonged "with *Lipaugus* and *Rhytipterna,* and not with the Pipridae." Apparently he did not consider the possibility that *Laniocera* and *Rhytipterna* might be tyrannid. Zimmer (1936), in describing the new genus *Pseudattila* said that "whether this genus [*Pseudattila*] belongs in the Tyrannidae or in the Cotingidae must await study of internal features. The genus *Attila* is in like predicament."

In external appearance most species of *Attila* are far more like the Tyrannidae than the Cotingidae. They are plain-colored, sexually monomorphic, and primarily insectivorous. The bill is broad at the base and strongly hooked at the tip. *Casiornis, Laniocera,* and *Rhytipterna* exhibit these tyrannid characters less strongly, but their outward appearance suggests tyrannid affinities. *Lipaugus* may later be added to this

group. The damaged specimen examined by me and the specimen studied by Garrod (1877b) seem to differ regarding M. obliquus ventralis and internal cartilages, but further examination is needed before the syringeal structure will be thoroughly known.

The similarity of the syrinx of the four "cotingas" listed above to that of *Myiarchus* is striking. Without assuming strong interdependence of several syringeal features, it is difficult to see how two groups of birds could evolve both external and internal similarities to such a degree.

The structure of the myiarchine syrinx does not provide many clues to the relationships of the group within the family. Externally their appearance suggests that their closest relatives might lie in the *Tyrannus* group.

6. The *Colopteryx* group have several features of the syrinx that are not found elsewhere. The most striking are the long dorsal extension of the pessulus, accompanied by dorsally incomplete elements, and the long, narrow, overlapping Mm. obliqui ventrales. These two features may well be funtionally interdependent. The group contains *Colopteryx, Oncostoma, Euscarthmornis, Hemitriccus, Myiornis,* and *Lophotriccus,* all of which were placed by Hellmayr in the Euscarthminae. In his linear arrangement no genera examined in this study were placed among the six above.

The flatbills, *Platyrinchus,* have a small mid-dorsal plate (but no pessulus) and long but not crossed Mm. obliqui ventrales, suggesting that they might belong in or near the *Colopteryx* group. The Mm. tracheolaterales extend further posteriad than in the *Colopteryx* group. Von Ihering (1904) believed *Platyrinchus* to be closely related to *Oncostoma* and *Hemitriccus*, a view supported by von Berlepsch (1905). Hellmayr (1927) restricted the subfamily Platyrinchinae to the flat-billed forms, *Cnipodectes, Tolmomyias, Rhynchocyclus, Platyrinchus,* and *Ramphotrigon.* I have not been able to obtain specimens of *Cnipodectes* and *Ramphotrigon* but the other three differ so strongly in their syringeal structure that one may seriously question the reliability of bill shape as a common character for the five genera.

Tolmomyias sulphurescens and *T. megacephalus* differ strikingly in syringeal cartilages and musculature. Zimmer (1939) transferred *megacephalus* to the genus *Ramphotrigon,* largely on the basis of coloration. The transfer of *megacephalus* out of *Tolmomyias,* at least, is supported by the syringeal morphology.

7. In the *Elaenia* group the syrinx is characterized by the presence of a well-fused drum and of M. obliquus lateralis. In most forms the well-developed M. obliquus ventralis originates on a median raphe attached to the drum. The internal cartilages are narrow curved bars, usually with flat ventral extensions. Included are *Elaenia, Suiriri, Camptostoma, Tyrannulus,* and *Phaeomyias.*

Elaenia gaimardi was moved from the Tyrannidae to the Pipridae by Ridgway (1905), solely on the basis of its pycnaspidean tarsus and basal syndactyly. He made it the type of a new genus *Elainopsis.* The new genus was not recognized by most subsequent authors, who have retained *gaimardi* in *Elaenia* or in *Myiopagis.* The latter genus was erected by Salvin and Godman (1888) for certain forms with specialized nostrils. The relative uniformity of syringeal structure among the nine species of *Elaenia* examined supports Hellmayr's (1927) contention that *Elaenia* is "a very natural genus."

The genera *Microtriccus* and *Tyranniscus* (perhaps only *nigrocapillus*) probably belong near the *Elaenia* group. Ridgway (1907, p. 339) transferred *Microtriccus*

[=*Ornithion*] along with *Tyrannulus*, to the Cotingidae on the basis of their pycnaspidean tarsi, but Hellmayr (1927) and most recent authors have retained both in the Tyrannidae. The syringeal cartilages of *Microtriccus* fit the *Elaenia* pattern closely, with a fully fused drum and flat extensions on the internal cartilages. *Microtriccus* differs from the *Elaenia* group in lacking M. obliquus lateralis. There is little to suggest whether *Microtriccus* diverged from the *Elaenia* line before the appearance of the lateral muscle or whether the muscle was lost secondarily. *Tyrannulus* has a suggestion of M. obliquus lateralis in the deep dorsal fibers of M. obliquus ventralis, the direction of which is different from that of the superficial fibers. More specimens of *Tyrannulus* are needed to determine the extent of individual variation in this muscle.

The two species of *Tyranniscus* examined differ so strikingly in syringeal morphology that I felt it necessary to verify the identity of the specimens through comparison with skins. One cannot help wondering if a thorough analysis of structural and behavioral characters of these and other species of *Tyranniscus* would not result in dividing the genus.

8. The syringeal morphology of the following genera does not provide much indication of their position within the Tyrannidae, but affects their family allocation, which has sometimes been questioned.

Euscarthmus. Ridgway (1907, p. 339), treating this genus as *Hapalocercus*, believed that it was "probably . . . formicarian in its affinities," largely on the basis of its taxaspidean tarsal envelope. Wetmore (1926) felt that *Euscarthmus* was "certainly not a true flycatcher," and placed the genus tentatively in the antbirds. Hellmayr (1927, p. 357) echoed Ridgway's remarks and called the position of *Euscarthmus* "quite uncertain," although he placed it in the Tyrannidae. The genus does not agree with any of the Furnarii in its syringeal structure, but does fit easily into the Tyrannidae. Its long, anteriorly situated drum and long, narrow internal cartilages are unlike those of any other genus that I have examined. In syringeal musculature *Euscarthmus* resembles *Inezia* and *Pogonotriccus*, but the similarities are not strong and all three have simple Mm. obliqui ventrales.

Stigmatura. This genus was placed by Ridgway (1907, p. 339) in the Formicariidae on the basis of its resemblance "in general form" to the antbird genus *Formicivora* [=*Neorhopias*], and Wetmore (1926) agreed with Ridgway's allocation of the genus. Hellmayr (1927, p. 379) included *Stigmatura* in the Tyrannidae, but suggested that it might belong in the Formicariidae. *Stigmatura* is typically tyrannid in its syrinx, with no resemblance to the Furnarii.

Habrura. Ridgway (1907, p. 339) felt that *Habrura* could not be a tyrannid and "might not be out of place in the Cotingidae," basing his opinion on the shape of the nostrils and the configuration of the tarsal envelope. Most other authorities have retained this genus in the Tyrannidae, although Hellmayr expressed skepticism that it belonged there. The syringeal structure of *Habrura* supports its inclusion in the Tyrannidae, but its placement within the family is not greatly aided by syringeal morphology. In the shape of the intrinsic muscles *Habrura* most resembles *Capsiempis* but the cartilages of both genera are of a type widely distributed in the family.

Mionectes and *Pipromorpha*. The peculiar syringeal structure of these two genera, with very small, ventrally located Mm. obliqui ventrales and extensive fusion of the

lower A-elements, is unlike other members of Hellmayr's subfamily Elaeniinae. The posterior ventral narrowing of the Mm. tracheolaterales probably cannot be taken as indicating relationships, for it occurs in others of the family, apparently unrelated to *Mionectes* and *Pipromorpha,* namely *Pachyramphus, Pyrocephalus* and *Colorhamphus.* The syringes of *Pipromorpha* and *Mionectes* are identical, considered in the light of the variability in the rest of the family, and support the merger of the two genera suggested by Todd (1921) and Hellmayr (1927).

Corythopis. This interesting genus of "ant-pipits," usually placed with *Conopophaga* in the family Conopophagidae, has been found (Ames et al., 1968) to be unrelated to the antbird-ovenbird assemblage and to be typically tyrannid in several features of its anatomy. The syrinx of *Corythopis* is notable for the peculiar shape of the internal cartilages, which are not far from those of *Leptotriccus sylvcolus.* There is little in the external anatomy to suggest a relationship between the two genera, so one may probably assume the slight similarity of internal cartilages to be convergent.

Pachyramphus and *Platypsaris.* The becards have been placed in the Cotingidae by all authors and I know of no one who has suggested that they might be tyrannid. Müller (1847) noticed the resemblance in syringeal musculature between *Pachyramphus rufus* and *Pyrocephalus rubinus,* but the resemblance does not extend to the cartilages. Suffice to say, the becards have several tyrannid features of the syrinx that are not found in the more typical members of the Cotingidae. Moreover they are plain-colored, only slightly sexually dimorphic, and primarily insectivorous. It is likely that a thorough investigation of many unrelated taxonomic characters would show that the becards are more closely related to the Tyrannidae than to *Cotinga, Pyroderus,* and others of the restricted family Cotingidae.

OXYRUNCIDAE.

The peculiar sharpbill (*Oxyruncus cristatus*) has a basically tyrannid syrinx, with oblique ventral intrinsic muscles and internal cartilages, but I cannot agree with Clark (1913) that its syrinx bears a "striking resemblance" to that of any particular genus of tyrannid, least of all to *Tyrannus* and *Sayornis.* The syringeal musculature of the sharpbill is strikingly like that of the becards (*Pachyramphus*) but there are substantial differences in the supporting cartilages. The type of musculature found in the sharpbill and the becards occurs elsewhere among the Tyrannidae, so the similarity should not be given too much weight.

MENURAE.

The lyrebirds (*Menura*) and scrub-birds (*Atrichornis*) are currently separated from the suborder Passeres primarily on the basis of their smaller number of syringeal muscles and the peculiarities of their pectoral apparatus and flight feathers. The lyrebirds and scrub-birds are more alike in syringeal structure than was previously inferred from the work of Garrod (1876), who reported finding only two pairs of

intrinsic muscles in *A. rufescens*. It is possible that the two species of *Atrichornis* differ in the number of syringeal muscles, but I am inclined to believe that Garrod overlooked a pair of muscles. Although the musculature is very close to the oscine pattern, there are major differences in the cartilages. In both muscles and cartilages, the Menurae lie well outside the range of variation shown by the vast array of recognized oscines. The syringeal evidence supports the osteological and pterylographic characters in separating the Menurae from the Passeres.

PASSERES OR "OSCINES".

The extreme homogeneity of the oscine syrinx strongly supports the present inclusion of the fifty-odd families in a single suborder. Detailed comment on the taxonomic relationships of the various families is beyond the scope of this paper, but some remarks on the supposed primitiveness of the syrinx in the larks and swallows are appropriate. No single group of oscines can be considered syringeally primitive, in the sense that the Menurae can be considered so. The features that distinguish the syrinx in the Alaudidae (absence of the pessulus) and Hirundinidae (double bronchial elements) were almost certainly not found in the syrinx of the ancestral oscine and must be considered adaptive modifications of unknown value. Although the larks and swallows do represent distinct and probably early offshoots of the main oscine stem, a contention supported by their syringeal structure and a number of other characters, the term "primitive" is inappropriate as applied to their syrinx.

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APPENDIX A

DATA FOR SPECIMENS OF THE SUBORDERS EURYLAIMI, FURNARII, TYRANNI AND MENURAE

In this appendix are listed the available data for all of the suboscine specimens examined in this study. The nomenclature and taxonomic order are drawn from the following sources: Eurylaimi, Peters (1951); Furnarii and Tyranni (New World families), Hellmayr (1924-28); Pittidae, Smythies (1940, 1960) and Mackworth-Praed and Grant (1955); Philepittidae, Rand (1936) and Amadon (1951); Acanthisittidae, Flemming (1953); Menurae, Cayley (1931).

Abbreviations

The institutions from which the specimens were obtained are indicated by the following abbreviations:

AMNH	American Museum of Natural History, New York, New York.
BM	British Museum (Natural History), London.
CM	Carnegie Museum, Pittsburgh, Pennsylvania
LSUMZ	Museum of Zoology, Louisiana State University, Baton Rouge, Louisiana.
MVZ	Museum of Vertebrate Zoology, University of California, Berkeley, California.
USNM	United States National Museum, Washington, D. C.
WGG	William G. George Collection. Southern Illinois University, Carbondale, Illinois.
YPM	Peabody Museum of Natural History, Yale University, New Haven, Connecticut.

Suborder Eurylaimidae

FAMILY EURYLAIMIDAE. BROADBILLS.

Smithornis capensis (A. Smith)	YPM 1608; Tanganyika; Sep 1961; Coll: G. H. Heinrich.
Smithornis rufolateralis G. R. Gray	AMNH (no number); Congo; 7 Sep 1930; Coll: J. P. Chapin.
Cymbirhynchus macrorhynchus (Gmelin)	USNM 290033; Sumatra; 1921; Coll: H. C. Keller.
Eurylaimus javanicus Horsfield	USNM 290082; Sumatra; 1921; Coll: H. H. Keller.
Serilophus lunatus (Gould)	USNM 439900; Thailand; 24 May 1955; Coll: R. E. Elbel.
Psarisomus dalhousei (Jameson)	USNM 429906; Borneo; 2 Aug 1953; Coll: R. Traub.
Calyptomena whiteheadi Sharpe	USNM 429241; Borneo; 1953; Coll: R. E. Elbel.

SUBORDER FURNARII

FAMILY DENDROCOLAPTIDAE. WOODCREEPERS.

Dendrocincla fuliginosa (Vieillot)	YPM 1017; Colombia, Magdalena; 21 May 1961; Coll: M. A. Carriker, Jr.
Sittasomus griseicapillus (Vieillot)	AMNH (no number); Brazil; 1 Mar 1930; Coll: E. Kaempfer.
Glyphorhynchus spirurus (Vieillot) ♀	YPM 1071; Colombia, Magdalena; 8 Apr 1961; Coll: M. A. Carriker, Jr.
Glyphorhynchus spirurus (Vieillot) ♂	YPM 1802; Surinam; 26 Nov 1961; Coll: R. Freund.
Drymornis bridgesii (Eyton)	USNM 227568; Argentina, Victoria; 23 Dec 1920; Coll: A. Wetmore.
Xiphocolaptes promeropirhynchus (Lesson)	YPM 2089; Colombia, Santander; 10 Jan 1962; Coll: M. A. Carriker, Jr.
Xiphocolaptes major (Vieillot)	AMNH (no number); Brazil; date unknown; Coll: E. Kaempfer.
Dendrocolaptes platyrostris Spix	YPM 2284; Argentina, Misiones; 7 Jul 1961; Coll: P. S. Humphrey.
Xiphorhynchus picus (Gmelin)	YPM 2040; Colombia, Santander; 17 Apr 1962; Coll: M. A. Carriker, Jr.
Xiphorhynchus picus (Gmelin)	AMNH (no number); Brazil; 4 Apr 1963; Coll: E. T. Gilliard.
Lepidocolaptes souleyetii (Des Murs)	YPM 1022; Colombia, Magdalena; 24 May 1961; Coll: M. A. Carriker, Jr.
Lepidocolaptes affinis (Lafresnaye)	YPM 2058; Colombia, Santander; 4 Jan 1962; Coll: M. A. Carriker, Jr.
Lepidocolaptes albolineatus (Lafresnaye)	YPM 1813; Surinam; 3 Dec 1961; Coll: R. Freund.
Campylorhamphus trochilirostris (Lichtenstein) ♀	YPM 2277; Argentina, Misiones; 16 June 1961; Coll: P. S. Humphrey.

FAMILY FURNARIIDAE. OVENBIRDS.

Geositta cunicularia (Vieillot) ♀	YPM 3823; Argentina, Sta. Cruz; 11 Jan 1961; Coll: P. S. Humphrey.
Geositta cunicularia (Vieillot) ♂	YPM 3825; Argentina, Sta. Cruz; 11 Jan 1961; Coll: P. S. Humphrey.
Geositta cunicularia (Vieillot)	YPM 18; Chile; 1958; Coll: L. E. Peña.
Furnarius leucopus Swainson	AMNH (no number); Brazil; no other data.
Cinclodes patagonicus (Gmelin) ♀	YPM 2326; Argentina, Sta. Cruz; 1 Dec 1960; Coll: P. S. Humphrey.
Cinclodes patagonicus (Gmelin) ♂	YPM 2327; Argentina, Sta. Cruz; 1 Dec 1960; Coll: P. S. Humphrey.
Cinclodes fuscus (Vieillot)	YPM 2846; Argentina, Sta. Cruz; 26 Dec 1960; Coll: P. S. Humphrey.
Upucerthia dumetaria Geoff. St. Hilaire	YPM 3833; Argentina; 14 Jan 1961; Coll: P. S. Humphrey.
Limnornis curvirostris Gould	AMNH (no number); Brazil; no other data.
Aphastrura spinicauda (Gmelin)	YPM 9; Chile, Santiago; 20 Aug 1958; Coll: L. E. Peña.
Phleocryptes melanops (Vieillot)	YPM 2542; Argentina, Entre Rios; 1 Apr 1961; Coll: P. S. Humphrey.
Phleocryptes melanops (Vieillot)	AMNH (no number); Brazil; no other data.

Synallaxis cinerascens Temminck	YPM 2547; Argentina, Misiones; 11 Jul 1961; Coll: P. S. Humphrey.
Certhiaxis cinnamomea (Gmelin)	CM 65; Venezuela, Guarico; 10 Sep 1927; Coll: E. G. Holt.
Asthenes pyrrholeuca (Vieillot) ♂	YPM 2364; Argentina, Chubut; 19 June 1961; Coll: P. S. Humphrey
Phacellodomus rufifrons (Wied)	AMNH (no number); Brazil; no other data.
Phacellodomus striaticollis (Lafr. and D'Orb.)	YPM 2374; Argentina, Entre Rios; 30 Apr 1961; Coll: P. S. Humphrey.
Anumbius anumbi (Vieillot)	YPM 2304; Argentina, Buenos Aires; 28 Oct 1960; Coll: P. S. Humphrey.
Pseudocolaptes boissoneautii (Lafr.)	YPM 2088; Colombia, Santander; 9 Jan 1962; Coll: M. A. Carriker, Jr.
Pseudoseisura lophotes (Reichenbach)	YPM 2397; Argentina, Rio Negro; 12 Feb 1961; Coll: P. S. Humphrey.
Pseudoseisura gutteralis (Lafr. and D'Orb.) ♂	YPM 2409; Argentina, Chubut; 16 Jan 1961; Coll: P. S. Humphrey.
Anabazenops fuscus (Vieillot)	AMNH (no number); Brazil, Sta. Catarina; no other data.
Philydor rufus (Vieillot)	AMNH (no number); Brazil; no other data.
Automolus ochrolaemus (Tschudi)	AMNH (field no.) 726; Nicaragua; 1917; Col: W. deW. Miller.
Heliobletus contaminatus Berlepsch	AMNH (no number); no data.
Xenops minutus (Sparrman)	YPM 1042; Colombia, Santander; 10 Mar 1961; Coll: M. A. Carriker, Jr.
Megaxenops parnaguae Reiser	AMNH (field no.) 6113; Brazil, Bahia; 12 Aug 1927; Coll: E. Kaempfer.
Pygarrhicus albogularis (King)	YPM 56; Chile, Malleco; 30-31 Dec 1958; Coll: L. E. Peña.
Sclerurus guatemalensis (Hartlaub)	USNM 431001; Panamá; 6 Mar 1959; Coll: unknown.

FAMILY FORMICARIIDAE. ANTBIRDS.

Cymbilaimus lineatus (Leach) ♂	AMNH (field no.) 750; Nicaragua; 1917; Coll: W. deW. Miller.
Cymbilaimus lineatus (Leach) ♀	AMNH (field no.) 764; Nicaragua; 1917; Coll: W. deW. Miller
Hypoedaleus guttatus (Vieillot)	YPM 2650; Argentina; Misiones; 12 Feb 1961; Coll: P. S. Humphrey.
Taraba major (Vieillot) ♂	AMNH (field no.) 765; Nicaragua; 1917; Coll: W. deW. Miller
Sakesphorus canadensis (Linnaeus)	AMNH (no number); British Guiana; "10/12/37;" Coll: R. Snediger.
Thamnophilus doliatus (Linnaeus) ♀	YPM 1055; Colombia, Santander; 22 Mar 1961; Coll: M. A. Carriker, Jr.
Thamnophilus doliatus (Linnaeus) ♀	AMNH (no number); Nicaragua; 1913; Coll: W. deW. Miller.
Thamnophilus punctatus (Shaw)	AMNH (field no.) 738; Nicaragua; 1917; Coll: W. deW. Miller
Thamnophilus punctatus (Shaw)	YPM 999; Colombia, Magdalena; 17 May 1961; Coll: M. A. Carriker, Jr.
Thamnophilus punctatus (Shaw)	YPM 1000; Colombia, Magdalena; 17 May 1961; Coll: M. A. Carriker, Jr.
Thamnophilus caerulescens Vieillot	YPM 2497; Argentina, Corrientes; 18 May 1961; Coll; P. S. Humphrey.
Pygiptila stellaris (Spix)	USNM 319838; Brazil, Amazonas; 12 Jan 1931; Coll: E. G. Holt.

Dysithamnus mentalis (Temminck)	YPM 1675; Colombia, Santander; 27 Jul 1961; Coll: M. A. Carriker, Jr.
Dysithamnus mentalis (Temminck)	YPM 1676; Colombia, Santander; 27 Jul 1961; Coll: M. A. Carriker, Jr.
Thamnomanes caesius (Temminck)	AMNH (no number); Brazil, Espirito Santo; 3 Nov 1929; Coll: E. Kaempfer.
Myrmotherula cherriei Berl. and Hart. ♀	USNM 318733; Venezuela, Ter. Fed. Amaz.; 4 Jan 1930; Coll: E. G. Holt.
Myrmotherula axillaris (Vieillot)	USNM 318722; Venezuela, Ter. Fed. Amaz.; 3 Jan 1930; Coll: E. G. Holt.
Myrmotherula axillaris (Vieillot)	YPM 1013; Colombia, Magdalena; 21 May 1961; Coll: M. A. Carriker, Jr.
Myrmotherula axillaris (Vieillot)	YPM 1014; Colombia, Magdalena; 22 May 1961; Coll: M. A. Carriker, Jr.
Herpsilochmus pileatus (Litchtenstein)	AMNH (no number); Brazil, Bahia; 5 May 1928; Coll: W. deW. Miller.
Microrhopias quixensis (Cornalia)	AMNH (field no.) 806; Nicaragua; 1917; Coll: W. deW. Miller.
Neorhopias grisea (Boddaert)	AMNH (no number); Brazil, Bahia; 3 May 1928; Coll: E. Kaempfer.
Neorhopias rufa (Wied)	YPM 1862; Surinam; 10 Dec 1961; Coll: R. Freund.
Drymophila squamata (Lichtenstein)	AMNH (no number); Brazil; date unknown; Coll: E. Kaempfer.
Cercomacra tyrannina (Sclater) ♂	AMNH (field no.) 829; Nicaragua; 1917; Coll: W. deW. Miller.
Cercomacra tyrannina (Sclater) ♂	AMNH (field no.) 830; Nicaragua; 1917; Coll: W. deW. Miller.
Pyriglena leucoptera (Vieillot)	AMNH (no number); Brazil, Bahia; 22 Jun 1926; Coll: E. Kaempfer.
Hypocnemis flavescens (Sclater)	USNM 319828; Brazil; 21 Nov 1930; N. G. S. Brazil-Venez. Exp.
Hypocnemoides melanopogon (Sclater)	USNM 318724; Venezuela, Bolivar; 30 Dec 1929; Coll: E. G. Holt.
Myrmeciza exsul Sclater	YPM 1001; Colombia, Magdalena; 17 May 1961; Coll: M. A. Carriker, Jr.
Myrmoderus squamosus (Pelzeln)	AMNH (no number); Brazil; date unknown; Coll: E. Kaempfer.
Formicarius analis (Lafr. and D'Orb.)	AMNH (no number); Nicaragua; 12 May 1917; Coll: W. deW. Miller
Formicarius analis (Lafr. and D'Orb.)	YPM 987; Colombia, Magdalena; 15 May 1961; Coll: M. A. Carriker, Jr.
Formicarius analis (Lafr. and D'Orb.)	YPM 988; Colombia, Magdalena; 17 May 1961; Coll: M. A. Carriker, Jr.
Formicarius analis (Lafr. and D'Orb.)	YPM 2120; Mexico, Oaxaca; 17 Mar 1962; Coll: W. J. Schaldach, Jr.
Chamaeza brevicauda (Vieillot) ♀	YPM 2457; Argentina, Corrientes; 20 May 1961; Coll: P. S. Humphrey.
Pithys albifrons (Linnaeus)	AMNH (no number); British Guiana; 1927; Coll: A. Lang.
Gymnopithys bicolor (Lawrence)	USNM 225008; Panamá; date unknown; Coll: E. A. Goldman.
Hylophylax naevioides (Lafresnaye) ♂	AMNH (no number); Nicaragua; 1913; Coll: W. deW. Miller.
Hylophylax naevioides (Lafresnaye) ♀	AMNH (field no.) 751; Nicaragua; 1917; Coll: W. deW. Miller.
Grallaria varia (Boddaert)	YPM 2475; Argentina, Corrientes; 12 May 1961; Coll: P. S. Humphrey.
Grallaria perspicillata Lawrence	YPM 1002; Colombia, Magdalena; 17 May 1961; Coll: M. A. Carriker, Jr.
Grallaria perspicillata Lawrence ♂	YPM 1068; Colombia, Magdalena; 3 Apr 1961; Coll: M. A. Carriker, Jr.

Grallaria ochroleuca (Wied)	YPM 2476; Argentina, Misiones; 2 Jul 1961; Coll: P. S. Humphrey.
Conopophaga lineata (Wied)	AMNH (no number); Brazil; date unknown; Coll: E. Kaempfer.
Conopophaga lineata (Wied) ♂	YPM 2550; Argentina, Corrientes; 10 May 1961; Coll: P. S. Humphrey.
Conopophaga lineata (Wied)	YPM 2551; Argentina, Corrientes; 10 May 1961; Coll: P. S. Humphrey.
Conopophaga lineata (Wied)	YPM 2552; Argentina, Corrientes; 10 May 1961; Coll: P. S. Humphrey.
Conopophaga roberti Hellmayr	USNM 195100; Brazil, Pará; June 1963; Coll: P. S. Humphrey.
Conopophaga roberti Hellmayr	USNM 195954; Brazil, Pará; Jun 1963; Coll: P. S. Humphrey.
Conopophaga roberti Hellmayr	USNM 196021; Brazil, Pará; Jun 1963; Coll: P. S. Humphrey.

FAMILY RHINOCRYPTIDAE. TAPACULOS.

Pteroptochos tarnii (King)	YPM 2566; Argentina, Rio Negro; 2 Feb 1961; Coll: P. S. Humphrey.
Pteroptochos tarnii (King)	YPM 2569; Argentina, Rio Negro; 2 Feb 1961; Coll: P. S. Humphrey.
Pteroptochos megapodius Kittlitz	YPM 63; Chile; 1958; Coll: I. E. Peña.
Scelorchilus rubecula (Kittlitz)	YPM 53; Chile, Malleco; 23 Jan 1959; Coll: L. E. Peña.
Rhinocrypta lanceolata (Geoff. Saint Hilaire)	USNM 227619; Argentina; 25 Nov 1920; Coll: A. Wetmore.
Rhinocrypta lanceolata (Geoff. Saint Hilaire)	YPM 2570; Argentina, Rio Negro; 12 Feb 1961; Coll: P. S. Humphrey.
Teledromas fuscus (Scl. and Salv.) ad ♂	USNM 227597; Argentina, Gen. Roca; 25 Nov 1920; Coll: A. Wetmore.
Melanopareia maximilliani (D'Orbigny)	USNM 227944; Argentina, Tucumán; 17 Apr 1921; Coll: A. Wetmore.
Scytalopus magellanicus (Gmelin)	YPM 52; Chile; 1958; Coll: L. E. Peña.
Triptorhinus paradoxus (Kittlitz)	YPM 69; Chile, Maulé; Jan 1959; Coll: L. E. Peña.

SUBORDER TYRANNI

FAMILY COTINGIDAE. COTINGAS.

Phoenicircus carnifex (Linnaeus) ♀	USNM (field no.) 198735; Brazil, Para, Belem; 4 Sep 1964; Coll: P. S. Humphrey.
Heliochera rubrocristata (Lafr. and D'Orb.)	New York Zool. Soc.; no data; Coll: C. W. Beebe.
Cotinga amabilis Gould	YPM 2127; Mexico, Oaxaca; 21 Mar 1962; Coll: W. J. Schaldach, Jr.
Cotinga maculata (Müller)	New York Zool. Soc.; no data; Coll: C. W. Beebe.
Xipholena punicea (Pallas)	AMNH (no number); British Guiana; 2 Feb 1923; Coll: Lang and Varr.
Carpodectes nitidus Salvin	USNM 19845; Costa Rica; 28 Mar 1905; Coll: R. Ridgway.
Euchlornis jucunda (Sclater) ♂	YPM 319; Ecuador; 1 Jan 1958; Coll: M. Erlanger.
Euchlornis aureopectus (Lafresnaye)	AMNH (no number); cage bird; 2 May 1938; New York Zool. Soc.

Euchlornis aureopectus (Lafresnaye)	YPM 2076; Colombia, Santander; 8 Jan 1962; Coll: M. A. Carriker, Jr.
Iodopleura isabellae (Shaw and Nodder)	MCZ (no number); Brazil, Para, Belem; Aug 1961; Coll: J. Hidasi.
Attila spadiceus (Gmelin)	YPM 2130; Mexico, Oaxaca; 21 Mar 1962; Coll: W. J. Schaldach, Jr.
Attila spadiceus (Gmelin)	AMNH (field no.) 866; Nicaragua; 1917; Coll: W. deW. Miller.
Attila cinnamomeus (Gmelin) ♀	USNM (field no.) 198365; Brazil, Para, Belem; 13 Aug 1964; Coll: P. S. Humphrey.
Casiornis rufa Vieillot	USNM 227189; Argentina, Chaco; 21 Jul 1920; Coll: A. Wetmore.
Laniocera rufescens (Sclater)	YPM 986; Colombia, Santander; 16 May 1961; Coll: M. A. Carriker, Jr.
Rhytipterna holerythra (Scl. and Salv.)	YPM 1074; Colombia, Magdalena; 8 Apr 1961; Coll: M. A. Carriker, Jr.
Rhytipterna holerythra (Scl. and Salv.)	YPM 1092; Colombia, Magdalena; 8 Apr 1961; Coll: M. A. Carriker, Jr.
Rhytipterna holerythra (Scl. and Salv.) ♂	AMNH (field no.) 743; Nicaragua; 1917; Coll: W. deW. Miller.
Lipaugus unirufus Sclater	YPM 1005; Colombia, Magdalena; 17 May 1961; Coll: M. A. Carriker, Jr.
Pachyramphus rufus (Boddaert)	YPM 863; Colombia, Santander; 24 Jan 1961; Coll: M. A. Carriker, Jr.
Pachyramphus polychopterus (Vieillot)	YPM 1041; Colombia, Santander; 10 May 1961; Coll: M. A. Carriker, Jr.
Pachyramphus polychopterus (Vieillot)	AMNH (no number); Nicaragua; 1917; Coll: W. deW. Miller.
Pachyramphus viridis (Vieillot)	YPM 2577; Argentina, Misiones; 2 Jul 1961; Coll: P. S. Humphrey.
Platypsaris aglaiae (Lafresnaye) ad ♀	YPM 1531; Mexico, Vera Cruz; 1962; Coll: R. W. Dickerman.
Platypsaris aglaiae (Lafresnaye) ad ♀	AMNH (field no.) 1174; Nicaragua; 1917; Coll: W. deW. Miller.
Platypsaris aglaiae (Lafresnaye)	AMNH (field no.) 1160; Nicaragua; 1917; Coll: W. deW. Miller.
Tityra semifasciata (Spix) ♀	YPM (no number); Mexico, Campeche; 16 Jul 1962; Coll: T. E. Lovejoy.
Tityra inquisitor (Lichtenstein)	YPM 2579; Argentina, Misiones; 21 Jun 1961; Coll: P. S. Humphrey.
Tityra cayana (Linnaeus)	YPM 1817; Surinam; 3 Dec 1961; Col: R. Freund.
Querula purpurata (Müller)	USNM 343943; Panamá; 15 Apr 1937; Col: W. deW. Miller.
Pyroderus scutatus (Shaw) ♂	YPM 3608; Argentina, Misiones; 7 Jul 1961; Coll: P. S. Humphrey.
Pyroderus scutatus (Shaw)	USNM 321594; no data.
Cephalopterus ornatus Geoff. Saint Hilaire	USNM 19802; Costa Rica; 1 May 1905; Coll. R. Ridgway.
Perissocephalus tricolor (Müller)	AMNH (no number); Venezuela; 8 Feb 1938; Coll: W. Phelps.
Gymnoderus foetidus (Linnaeus)	USNM 32160; no data.
Conioptilon mcilhennyi Lowery and O'Neill ♀	LSUMZ 42871; Peru, Loreto; 21 Mar 1965; Coll: J. P. O'Neill.
Procnias tricarunculata (J. and E. Verreaux)	USNM 413214; Panamá, Bocas del Toro; 17 Jan 1960; Coll: unknown.
Rupicola rupicola (Linnaeus) ad ♂	AMNH (no number); British Guiana; 26 Feb 1961; Coll: E. T. Gilliard.

Rupicola rupicola (Linnaeus)	New York Zool. Soc. (no number); no data; Coll: C. W. Beebe.
Rupicola rupicola (Linnaeus) ♂	YPM (no number); USA, Pennsylvania; captive bird; 10 Apr 1962; Coll: K. C. Parkes.

FAMILY PIPRIDAE. MANAKINS.

Piprites chloris (Temminck)	YPM 2582; Argentina, Misiones; 13 Jun 1961; Coll: P. S. Humphrey.
Pipra mentalis Sclater	YPM 2121; Mexico; Oaxaca; 28 Mar 1962; Coll: W. J. Schaldach, Jr.
Pipra mentalis Sclater ♂	AMNH (field no.) 784; Nicaragua; 1917; Coll: W. deW. Miller.
Pipra erythrocephala (Linnaeus)	YPM 985; Colombia, Magdalena; 16 May 1961; Coll: M. A. Carriker, Jr.
Chiroxiphia lanceolata (Wagler)	USNM 343871; Panamá; 16 Feb 1937; Coll: Miller and Wheeler.
Chiroxiphia caudata (Shaw and Nodder)	YPM 2587; Argentina, Corrientes; 18 May 1961; Coll: P. S. Humphrey.
Chiroxiphia caudata (Shaw and Nodder)	AMNH (no number); Brazil; 22 Sep 1928; Coll: E. Kaempfer.
Ilicura militaris Parzudaki	BM 1936-3-5-1; cage bird; died 11 Mar 1936; Coll: A. Ezra.
Corapipo leucorrhoa (Sclater) ♂	USNM 19938; Costa Rica; 1908; Coll: R. Ridgway.
Manacus vitellinus (Gould)	USNM 343873; Panamá; 20 Feb 1937; Coll: Miller and Wheeler.
Manacus candei (Parzudaki)	YPM 2164; Mexico, Oaxaca; 29 Mar 1962; Coll: W. J. Schaldach, Jr.
Schiffornis virescens (Lafresnaye) ♀	YPM 2603; Argentina Corrientes; 11 May 1961; Coll: P. S. Humphrey.
Schiffornis turdinus (Wied)	AMNH (field no.) 892; Nicaragua; 1917; Coll: W. deW. Miller.
Schiffornis turdinus (Wied) ♂	USNM (field no.) 196400; Brazil, Pará; 2 Jul 1964; Coll: P. S. Humphrey.
Schiffornis turdinus (Wied) ♀	USNM (field no.) 196529; Brazil, Pará; 8 Jul 1964; Coll: P. S. Humphrey.

FAMILY TYRANNIDAE. TYRANT FLYCATCHERS.

SUBFAMILY FLUVICOLINAE.

Agriornis livida (Kittlitz)	YPM 21; Chile, Nagué; Sep 1958; Coll: L. E. Peña.
Agriornis microptera Gould	YPM 2613; Argentina, Chubut; 1 Nov 1960; Coll: P. S. Humphrey.
Xolmis coronata (Vieillot) ♂	YPM 2819; Argentina, Buenos Aires; 26 Oct 1960; Coll: P. S. Humphrey.
Xolmis irupero (Vieillot) ♂	YPM 2823; Argentina, Buenos Aires; 24 Oct 1960; Coll: P. S. Humphrey.
Xolmis pyrope (Kittlitz)	YPM 14; Chile; 1958; Coll: L. E. Peña.
Xolmis pyrope (Kittlitz) ♀	YPM 2832; Argentina, Chubut; 20 Jan 1961; Coll: P. S. Humphrey.
Muscisaxicola albilora Lafresnaye	YPM 2712; Argentina, Chubut; 18 Jan 1961; Coll: P. S. Humphrey.
Muscisaxicola maculirostris Lafr. and D'Orb. ♂	YPM 2856; Argentina, Santa Cruz; 23 Dec 1960; Coll: P. S. Humphrey.

Lessonia rufa (Gmelin)	YPM 10; Chile; 1958; Coll: L. E. Peña.
Neoxolmis rufiventris (Vieillot) ♂	YPM 2736; Argentina, Santa Cruz; 14 Nov 1960; Coll: P. S. Humphrey.
Neoxolmis rufiventris (Vieillot) ♀	YPM 2739; Argentina, Santa Cruz; 12 Jan 1961; Coll: P. S. Humphrey.
Ochthoeca fumicolor Sclater	AMNH (field no.) 692; Peru; no other data; Coll: E. Heller.
Ochthoeca fumicolor Sclater	YPM 973; Colombia; 3 May 1961; Coll: M. A. Carriker.
Sayornis phoebe (Latham)	YPM (no number); USA, Connecticut; Jul 1960; Coll: D. H. Parsons.
Sayornis phoebe (Latham) ad ♂	YPM (field no.) J-766; USA, Connecticut; 28 Aug 1963; Coll: P. L. Ames.
Sayornis phoebe (Latham) imm ♀	YPM (field no.) J-767; USA, Connecticut; 28 Aug 1963; Coll: P. L. Ames.
Sayornis nigricans (Swainson)	USNM 85224; USA, California; 1881; Coll: L. Belding.
Sayornis saya (Bonaparte)	YPM 283; USA, Colorado; 18 Jul 1953; Coll: D. H. Parsons.
Colonia colonus (Vieillot)	AMNH (no number); Panamá; 1924; Coll: C. M. Breder.
Colonia colonus (Vieillot)	AMNH (no number); Panamá; 23 Aug 1923; Coll: unknown.
Colonia colonus (Vieillot)	YPM 2634; Argentina, Misiones; 19 Jan 1961; Coll: P. S. Humphrey.
Gubernetes yetapa (Vieillot)	YPM 2655; Argentina, Corrientes; 19 May 1961; Coll: P. S. Humphrey.
Gubernetes yetapa (Vieillot)	YPM 2654; Argentina, Corrientes; 10 May 1961; Coll: P. S. Humphrey.
Yetapa risora (Vieillot)	USNM 227318; Argentina, Formosa; 18 Aug 1920; Coll: A. Wetmore.
Knipolegus nigerrimus (Vieillot)	AMNH (no number); Brazil; no other data.
Knipolegus cyanirostris (Vieillot)	YPM 2680; Argentina, Misiones; 7 Jul 1961; Coll: P. S. Humphrey.
Knipolegus cyanirostris (Vieillot)	YPM 2681; Argentina, Misiones; 11 Jul 1961; Coll: P. S. Humphrey.
Knipolegus cyanirostris (Vieillot)	YPM 2678; Argentina, Misiones; 8 Jun 1961; Coll: P. S. Humphrey.
Phaeotriccus hudsoni (Sclater)	USNM 227585; Argentina, Victoria; 29 Dec 1920; Coll: A. Wetmore.
Entotriccus striaticeps (Lafr. and D'Orb.)	USNM 227313; Argentina; 13 Aug 1920; Coll: A Wetmore.
Lichenops perspicillata (Gmelin)	YPM 2668; Argentina, Buenos Aires; 24 Oct 1960; Coll: P. S. Humphrey.
Muscipipra vetula (Lichtenstein)	AMNH (no number); Brazil, Paraná; 30 Mar 1030; Coll: E. Kaempfer.
Fluvicola climazura (Vieillot)	AMNH (field no.) 3048; Brazil, Piauí; 8 Jun 1926; Coll: E. Kaempfer.
Arundinicola leucocephala (Linnaeus)	USNM 321638; no data.
Pyrocephalus rubinus (Boddaert) ♂	YPM 2177; Mexico, Campeche; 9 Apr 1962; Coll: E. C. Migdalski.
Pyrocephalus rubinus (Boddaert)	YPM 2176; Mexico, Campeche; 9 Apr 1962; Coll: E. C. Migdalski.
Pyrocephalus rubinus (Boddaert) ♂	YPM 804; Colombia, Magdalena; 27 Jan 1961; Coll: M. A. Carriker, Jr.
Pyrocephalus rubinus (Boddaert) ♀	YPM 2768; Argentina, Misiones; 17 Jun 1961; Coll: P. S. Humphrey.
Pyrocephalus rubinus (Boddaert)	YPM 2766; Argentina, Entre Rios; 1 Apr 1961; Coll: P. S. Humphrey.

Muscigralla brevicauda Lafr. and D'Orb.	AMNH (no number); Peru, Puna Is.; 11 Jul 1932; Coll: unknown.
Satrapa icterophrys (Vieillot)	YPM 2770; Argentina, Entre Rios; 29 Mar 1961; Coll: P. S. Humphrey.
Satrapa icterophrys (Vieillot)	AMNH (no number); Brazil, Rio Grande do Sul; 15 Oct 1928; Coll: E. Kaempfer.
Machetornis rixosa (Vieillot)	YPM 2705; Argentina, Entre Rios; 29 Mar 1961; Coll: P. S. Humphrey.
Machetornis rixosa (Vieillot)	YPM 2709; Argentina, Entre Rios; 30 Apr 1961; Coll: P. S. Humphrey.
Machetornis rixosa (Vieillot)	AMNH (no number); "Brazil or Paraguay;" no other data.

SUBFAMILY TYRANNINAE

Muscivora tyrannus (Linnaeus)	AMNH (no number); Brazil, Paraná; 8 Mar 1962; Coll: E. Kaempfer.
Tyrannus tyrannus (Linnaeus) ♂	YPM 706; USA, Connecticut; 24 May 1961; Coll: D. H. Parsons.
Tyrannus tyrannus (Linnaeus) ♂	YPM (field no.) J-761; USA, Connecticut; date unknown; Coll: D. H. Parsons.
Tyrannus tyrannus (Linnaeus) ♂	YPM (no number); USA, Connecticut; 27 May 1961; Coll: D. H. Parsons.
Tyrannus albogularis Burmeister	YPM 1788; Surinam; 23 Nov 1961; Coll: R. Freund.
Tyrannus melancholicus Vieillot	YPM 1797; Surinam; 25 Nov 1961; Coll: R. Freund.
Tyrannus dominicensis (Gmelin)	YPM 3914; USA, Florida; 12 May 1962; Coll: A. Pflueger.
Empidonomus aurantioatrocristatus (Lafr. and D'Orb.)	YPM 2652; Argentina, Rio Negro; 12 Feb 1961; Coll: P. S. Humphrey.
Legatus leucophaius (Vieillot) ♀	YPM 2136; Mexico, Oaxaca; 22 Mar 1962; Coll: W. J. Schaldach, Jr.
Sirystes sibilator (Vieillot)	YPM 2790; Argentina, Misiones; 11 Jun 1961; Coll: P. S. Humphrey.
Sirystes sibilator (Vieillot)	YPM 2791; Argentina, Misiones; 16 Jun 1961; Coll: P. S. Humphrey.
Myiodynastes luteiventris Sclater	YPM 1048; Colombia, Santander; 29 Apr 1961; Coll: M. A. Carriker, Jr.
Myiodynastes luteiventris Sclater	YPM 1047; Colombia, Santander; 14 Mar 1961; Coll: M. A. Carriker, Jr.
Myiodynastes luteiventris Sclater	WGG 879; USA, Arizona; date unknown; Coll: W. G. George.
Myiodynastes bairdii Gambel	New York Zoological Society; 22 Dec 1962; Col: P. L. Ames.
Megarhynchus pitangua (Linnaeus)	YPM 1550; Mexico, Santa Ana; 7 Jun 1957; Coll: A. Starrett.
Conopias trivirgata (Wied)	YPM 2683; Argentina, Misiones; 11 Jun 1961; Coll: P. S. Humphrey.
Myiozetetes cayanensis (Linnaeus)	YPM 1844; Surinam; 6 Dec 1961; Coll: R. Freund.
Myiozetetes cayanensis (Linnaeus)	YPM 1769; Colombia, Santander; 26 Nov 1961; Coll: M. A. Carriker, Jr.
Myiozetetes cayanensis (Linnaeus)	YPM 2024; Colombia, Magdalena; 22 Feb 1962; Coll: M. A. Carriker, Jr.
Myiozetetes similis (Spix)	YPM 1543; Mexico, Vera Cruz; 12 Jul 1961; Coll: A. R. Phillips.
Myiozetetes similis (Spix)	YPM 2174; Mexico, Campeche; 9 Apr 1962; Coll: M. A. Carriker, Jr.
Myiozetetes similis (Spix)	YPM 1021; Colombia, Magdalena; 24 May 1961; Coll: M. A. Carriker, Jr.

Myiozetetes granadensis Lawrence	AMNH (field no.) 783; Nicaragua; 1917; Coll: W. deW. Miller.
Tyrannopsis sulphurea (Spix)	YPM 5146; New York Zool. Soc.; Feb 1964; Coll: J. Bell.
Pitangus sulphuratus (Linnaeus)	YPM 1533; Mexico, Vera Cruz; 26 Jul 1961; Coll: R. W. Dickerman.
Pitangus sulphuratus (Linnaeus)	AMNH (field no.) 1135; Nicaragua; 1917; Coll: W. deW. Miller.
Pitangus lictor Lichtenstein	YPM 1102; Colombia, Magdalena; 13 Apr 1961; Coll: M. A. Carriker, Jr.
Tolmarchus caudifasciatus (D'Orbigny)	USNM 291915; Cuba; 28 Jul 1928; Coll: P. Bartsch.

SUBFAMILY MYIARCHINAE.

Myiarchus crinitus (Linnaeus)	YPM (no number); USA, Connecticut; 27 May 1960; Coll: D. H. Parsons.
Myiarchus crinitus (Linnaeus)	YPM 759; USA, Connecticut; 5 Mar 1961; Coll: P. L. Ames.
Myiarchus crinitus (Linnaeus)	YPM 1122; USA, Connecticut; 19 May 1961; Coll: G. A. Clark, Jr.
Myiarchus brachyurus Ridgway	AMNH (no number); Nicaragua; 13 Jun 1917; Coll: W. deW. Miller.
Myiarchus tyrannulus (Müller)	YPM 2047; Colombia, Magdalena; 19 Apr 1962; Coll: M. A. Carriker, Jr.
Myiarchus ferox (Gmelin)	YPM 1868; Surinam; 10 Dec 1961; Coll: R. Freund.
Myiarchus tuberculifer (Lafr. and D'Orb.)	YPM 1040; Colombia, Santander; 10 Mar 1961; Coll: M. A. Carriker, Jr.
Myiarchus tuberculifer (Lafr. and D'Orb.)	YPM 1889; Surinam; 11 Dec 1961; Coll: R. Freund.
Nesotriccus ridgwayi Townsend	MVZ 3536; Cocos Island, 3 Oct 1965; Coll: R. W. Conard.
Eribates magnirostris (Gould)	USNM 20541; Galapagos Arch., Charles Is.; 8 Apr 1888; Coll: unknown.
Eribates magnirostris (Gould)	USNM 223306; Galapagos Arch., Indefatigable Is.; 12 Apr 1888; Coll: unknown.
Nuttallornis mesoleucus (Lichtenstein)	USNM 226305; USA, Arizona; 14 Jul 1918; Coll: A. Wetmore.
Myiochanes virens (Linnaeus)	YPM (no number); USA, Connecticut; date unknown; Coll: D. H. Parsons.
Myiochanes virens (Linnaeus)	YPM 4301; USA, Connecticut; 24 Sep 1963; Coll: P. L. Ames.
Myiochanes cinereus (Spix)	YPM 2641; Argentina, Misiones; 2 Jul 1961; Coll: P. S. Humphrey.
Blacicus carribaeus (D'Orbigny)	AMNH (no number); Dominican Rep.; 3 Sep 1922; Coll: R. C. Noble.
Empidonax flaviventris (Baird) ♀	YPM (no number); USA, Connecticut; 16 Sep 1961; Coll: D. H. Parsons.
Empidonax minimus (Baird)	YPM 700; USA, Connecticut; 23 May 1961; Coll: D. H. Parsons.
Empidonax minimus (Baird)	YPM 705; USA, Connecticut; 24 May 1961; Coll: P. L. Ames.
Empidonax minimus (Baird) ♂	YPM 4198; USA, Connecticut; 24 Sep 1963; Coll: P. L. Ames.
Empidonax difficilis Baird	YPM 1272; USA, California; 15 Aug 1961; Coll: P. L. Ames.
Empidonax albigularis Scl. and Salv. ♂	YPM 1543; Mexico, Mexico; date unknown; Coll: A. R. Phillips.
Empidonax oberholseri A. R. Phillips ♂	YPM 1544; Mexico, Mexico; 10 Nov 1961; Coll: R. W. Dickerman.

Aechmolophus mexicanus Zimmer ♂	Received from A. R. Phillips; Mexico, Morelos; 19 Jun 1961 1961; Coll: J. S. Rowley; Skin at Univ. Minn. Mus. Zool.
Cnemotriccus poecilurus (Sclater)	AMNH (field no.) 592; Peru; 1915; Coll: E. Heller.
Mitrephanes phaeocercus (Sclater)	MVZ (no number); Mexico, Nayarit; 28 Dec 1960; Coll: R. Stallcup.
Terenotriccus erythrurus (Cabanis)	AMNH (field no.) 867; no data.
Aphanotriccus capitalis (Salvin)	AMNH (field no.) 850; Costa Rica; 1917; Coll: W. deW. Miller.
Myiobius sulphureipygius (Sclater)	WGG 856; USA, Arizona; date unknown; Coll: W. G. George.
Myiobius atricaudatus Lawrence	USNM 343906; Panama; 20 Apr 1937; Coll: Miller and Wheeler.
Pyrrhomyias cinnamomeus (Lafr. and D'Orb.)	YPM 2057; Colombia, Magdalena; 4 Jan 1962; Coll: M. A. Carriker, Jr.
Myiophobus fasciatus (Müller)	YPM 1758; Colombia, Santander; 20 Nov 1961; Coll: M. A. Carriker, Jr.
Onychorhynchus coronatus (Müller) ♂	USNM 195241; Brazil; Jan 1963; Coll: P. S. Humphrey.
Onychorhynchus coronatus (Müller) ♀	USNM 195261; Brazil; Jan 1963; Coll: P. S. Humphrey.

SUBFAMILY PLATYRINCHINAE.

Platyrinchus mystaceus Vieillot	YPM 2758; Argentina, Misiones; 22 Jun 1961; Coll: P. S. Humphrey.
Platyrinchus cancrominus Sclater and Salvin	AMNH (no number); Nicaragua; 13 May 1917; Coll: W. deW. Miller.
Tolmomyias sulphurescens (Spix)	YPM (field no.) C-244; Argentina, Misiones; 19 Jun 1961; Coll: P. S. Humphrey.
Tolmomyias sulphurescens (Spix)	YPM (field no.) C-535; Argentina, Misiones; 3 Jul 1961; Coll: P. S. Humphrey.
Tolmomyias megacephalus (Swainson)	YPM 2769; Argentina, Misiones; 22 Jun 1961; Coll: P. S. Humphrey.
Rhynchocyclus olivaceus (Temminck)	YPM 1095; Colombia, Magdalena; 10 Apr 1961; Coll: M. A. Carriker, Jr.
Rhynchocyclus brevirostris (Cabanis)	YPM 2138; Mexico, Oaxaca; 26 Mar 1961; Coll: W. J. Schaldach, Jr.

SUBFAMILY EUSCARTHMINAE.

Todirostrum cinereum (Linnaeus)	YPM 1538; Mexico, Vera Cruz; 25 Aug 1961; Coll: A. R. Phillips.
Todirostrum sylvia (Desmarest)	YPM 1070; Colombia, Magdalena; 8 Apr 1961; Coll: M. A. Carriker, Jr.
Todirostrum sylvia (Desmarest)	YPM 1763; Colombia, Santander; 21 Nov 1961; Coll: M. A. Carriker, Jr.
Todirostrum plumbeiceps Lafresnaye	YPM 2803; Argentina, Misiones; 13 Jun 1961; Coll: P. S. Humphrey.
Oncostoma cinereigulare (Sclater)	AMNH (field no.) 849; Nicaragua; 1917; Coll: W. deW. Miller.
Euscarthmornis margaritaceiventer (Lafr. and D'Orb.)	USNM 227227; Argentina, Chaco; 9 Jul 1920; Coll: A. Wetmore.
Lophotriccus pileatus (Tschudi) ♀	USNM (no number); Panama; 3 Mar 1951; Coll: A. Wetmore.
Lophotriccus pileatus (Tschudi) ♀	USNM 428193; Panama; 3 Mar 1951; Coll: A. Wetmore.
Colopteryx galeatus (Boddaert)	YPM 1879; Surinam; 10 Dec 1961; Coll: R. Freund.

Myiornis auricularis (Vieillot)	YPM 2725; Argentina, Misiones; 17 Jun 1961; Coll: P. S. Humphrey.
Myiornis auricularis (Vieillot)	YPM 2727; Argentina, Misiones; 21 Jun 1961; Coll: P. S. Humphrey.
Hemitriccus diops (Temminck)	YPM 2662; Argentina, Misiones; 29 Jul 1961; Coll: P. S. Humphrey.
Pogonotriccus eximius (Temminck)	YPM 2759; Argentina, Misiones; 12 Jun 1961; Coll: P. S. Humphrey.
Pogonotriccus eximius (Temminck)	YPM 2762; Argentina, Misiones; 17 Jun 1961; Coll: P. S. Humphrey.
Leptotriccus sylviolus Cab. and Heine	YPM 2694; Argentina, Misiones; 10 Jul 1961; Coll: P. S. Humphrey.
Leptotriccus sylviolus Cab. and Heine	YPM 2693; Argentina, Misiones; 6 Jul 1961; Coll: P. S. Humphrey.
Phylloscartes ventralis (Temminck)	YPM 2753; Argentina, Misiones; 14 Jun 1961; Coll: P. S. Humphrey.
Capsiempis flaveola (Lichtenstein)	AMNH (no number); Nicaragua; 1913; Coll: W. deW. Miller.
Euscarthmus melorhyphus Wied	USNM 227325; Argentina; 23 July 1920; Coll: A. Wetmore.
Corythopis delalandi (Lesson)	YPM 2559; Argentina, Misiones; 30 Jun 1961; Coll: P. S. Humphrey.
Corythopis delalandi (Lesson)	YPM 2611; Argentina, Misiones; 23 Jun 1961; Coll: P. S. Humphrey.
Corythopis delalandi (Lesson)	YPM 2558; Argentina, Misiones; 22 Jun 1961; Coll: P. S. Humphrey.
Corythopis torquata Tschudi ♂	USNM (field no.) 198127; Brazil, Pará; 3 Aug 1964; Coll: P. S. Humphrey.
Corythopis torquata Tschudi ♂	USNM (field no.) 198562; Brazil, Pará; 21 Aug 1964; Coll: P. S. Humphrey.
Pseudocolopteryx sclateri (Oustalet)	USNM 227219; Argentina, Chaco; 27 Jul 1920; Coll: A. Wetmore.
Pseudocolopteryx flaviventris (Lafr. and D'Orb.)	USNM 227207; Argentina, Chaco: 22 Jul 1920; Coll: A. Wetmore.
Habrura pectoralis (Vieillot)	USNM 227218; Paraguay; 3 Sep 1920; Coll: A. Wetmore.
Habrura pectoralis (Vieillot)	YPM 2659; Argentina, Misiones; 21 Jul 1961; Coll: P. S. Humphrey.

SUBFAMILY SERPOPHAGINAE.

Tachuris rubigastra (Vieillot) ♂	YPM 3; Chile; 1958; Coll: L. E. Peña.
Tachuris rubigastra (Vieillot) ♀	YPM 4; Chile; 1958; Coll: L. E. Peña.
Tachuris rubigastra (Vieillot) ♂	YPM 2796; Argentina, Buenos Aires; 4 Aug 1961; Coll: P. S. Humphrey.
Tachuris rubigastra (Vieillot) ♀	YPM 2799; Argentina, Buenos Aires; 19 Aug 1961; Coll. P. S. Humphrey.
Spizitornis parulus (Kittlitz)	YPM 34; Chile; 1958; Coll: L. E. Peña.
Stigmatura budytoides (Lafr. and D'Orb.)	YPM 2783; Argentina, Rio Negro; 12 Feb 1961; Coll: P. S. Humphrey.
Serpophaga subcristata (Vieillot)	YPM 2777; Argentina; Garruchos; 11 May 1961; Coll: P. S. Humphrey.
Inezia subflava (Scl. and Salv.)	CM 71; Venezuela, Guarcia; 10 Sep 1927; Coll: E. G. Holt.
Mecocerculus leucophyrs (Lafr. and D'Orb.)	YPM 970; Colombia, Santander; 3 May 1961; Coll: M. A. Carriker, Jr.
Mecocerculus leucophrys (Lafr. and D'Orb.)	YPM 972; Colombia, Santander; 3 May 1961; Coll: M. A. Carriker, Jr.

Colorhamphus parvirostris (Darwin)	USNM 227983; Chile, Concón; 27 Apr 1927; Coll: A. Wetmore.
SUBFAMILY ELAENIINAE.	
Elaenia flavogaster (Thunberg)	YPM 2022; Colombia, Magdalena; 22 Feb 1962; Coll: M. A. Carriker, Jr.
Elaenia martinica (Linnaeus)	YPM 4035; Brit. West Indies, Antigua Is., 25 Mar 1963; Coll: Mrs. F. Olsen.
Elaenia albiceps (Lafr. and D'Orb.)	YPM 2641; Argentina, Tierra del Fuego; 28 Nov 1960; Coll: P. S. Humphrey.
Elaenia chiriquensis (Lawrence)	YPM 2021; Colombia, Santander; 22 Feb 1962; Coll: M. A. Carriker, Jr.
Elaenia chiriquensis (Lawrence)	YPM 1110; Colombia, Santander; 29 Apr 1961; Coll: M. A. Carriker, Jr.
Elaenia chiriquensis (Lawrence)	YPM 1111; Colombia, Santander; 29 Apr 1961; Coll: M. A. Carriker, Jr.
Elaenia obscura (Lafr. and D'Orb.)	YPM 1732; Colombia, Santander; 12 Oct 1961; Coll: M. A. Carriker, Jr.
Elaenia fallax Sclater ♂	YPM 197; Haiti; 5 Mar 1959; Coll: P. S. Humphrey.
Elaenia fallax Sclater ♀	YPM 196; Haiti; 5 Mar 1959; Coll: P. S. Humphrey.
Elaenia gaimardi (D'Orbigny)	YPM 1895; Surinam; 10 Dec 1961; Coll: R. Freund.
Elaenia viridicata (Vieillot)	AMNH (field no.) 1170; Nicaragua; 1913; Coll: W. deW. Miller.
Elaenia caniceps (Swainson)	YPM 2721; Argentina, Misiones; 2 Jul 1961; Coll: P. S. Humphrey.
Suiriri suiriri (Vieillot)	YPM 2788; Argentina, Entre Rios; 21 Apr 1961; Coll: P. S. Humphrey.
Suiriri affinis (Burmeister)	AMNH (no number); Brazil; 23 Jan 1926; Coll: E. Kaempfer.
Sublegatus modestus (Wied)	AMNH (no number); Brazil; 1915; Coll: E. Kaempfer.
Phaeomyias murina (Spix)	YPM 2038; Colombia, Magdalena; 17 Apr 1962; Coll: M. A. Carriker, Jr.
Phaeomyias murina (Spix)	YPM 2046; Colombia, Magdalena; 18 Apr 1962; Coll: M. A. Carriker, Jr.
Camptostoma obsoletum (Temminck)	YPM 2617; Argentina, Misiones; 7 Jun 1961; Coll: P. S. Humphrey.
Camptostoma imberbe Sclater	WGG 845; USA, Arizona; date unknown; Coll: W. G. George.
Tyranniscus chrysops (Sclater)	YPM 922; Colombia, Santander; 10 Mar 1922; Coll: M. A. Carriker, Jr.
Tyranniscus chrysops (Sclater)	YPM 2010; Colombia, Santander; 27 Jan 1962; Coll: M. A. Carriker, Jr.
Tyranniscus nigrocapillus (Lafresnaye)	YPM 2056; Colombia, Santander; 4 Jan 1962; Coll: M. A. Carriker, Jr.
Phyllomyias fasciatus (Thunberg)	USNM 227227; Argentina, Chaco; 27 Jul 1920; Coll: A. Wetmore.
Tyrannulus elatus (Latham)	YPM 1764; Colombia, Santander; 21 Nov 1961; Coll: M. A. Carriker, Jr.
Microtriccus semiflavus (Scl. and Salv.)	YPM 2141; Mexico, Oaxaca; 25 Mar 1962; Coll: W. J. Schaldach, Jr.
Microtriccus semiflavus (Scl. and Salv.)	YPM 1025; Colombia, Magdalena; 25 May 1961; Coll: M. A. Carriker, Jr.
Leptopogon (species unknown)	AMNH (field no.) 819; Nicaragua; 1913; Coll: W. deW. Miller.
Leptopogon (species unknown)	AMNH (field no.) 820; Nicaragua; 1913; Coll: W. deW. Miller.

Leptopogon (species unknown)	AMNH (field no.) 821; Nicaragua; 1913; Coll: W. deW. Miller.
Mionectes olivaceus Lawrence	USNM 430247; Peru; date unknown; Coll: H. F. Allard.
Pipromorpha oleaginea (Lichtenstein)	AMNH (field no.) 865; Nicaragua; 1913; Coll: W. deW. Miller.
Pipromorpha oleaginea (Lichtenstein)	AMNH (no number); Nicaragua; 1917; Coll: W. deW. Miller.
Pipromorpha oleaginea (Lichtenstein)	YPM 1765; Colombia, Santander; 21 Nov 1961; Coll: M. A. Carriker, Jr.

FAMILY OXYRUNCIDAE. SHARPBILL.

Oxyruncus cristatus (Gmelin)	BM (no number); cage bird; 19 Feb 1936; Coll: A. Ezra.

FAMILY PHYTOTOMIDAE. PLANTCUTTERS.

Phytotoma rare Molina	YPM 2874; Argentina, Chubut; 20 Jan 1961; Coll: P. S. Humphrey.
Phytotoma rare Molina	YPM 5; Chile, Nagué; 16-21 Sep 1958; Coll: L. E. Peña.
Phytotoma rutila Vieillot ♂	YPM 2884; Argentina, Buenos Aires; 24 Oct 1960; Coll: P. S. Humphrey.
Phytotoma rutila Vieillot ♀	YPM 2885; Argentina, Buenos Aires; 24 Oct 1960; Coll: P. S. Humphrey.

FAMILY PITTIDAE. PITTAS.

Pitta reichenowi Madarasz	AMNH (no number); Africa, Congo; 11 Oct 1930; Coll: J. P. Chapin.
Pitta boschi Müller and Schlegel	USNM 290038; Sumatra; 1926; K. C. Heller.
Pitta erythrogaster Temminck	AMNH (no number); New Guinea, New Britain; no other data.
Pitta atricapilla Lesson	AMNH (no number); cage bird; 1929; New York Zool. Soc.

FAMILY PHILEPITTIDAE. ASITIES AND FALSE SUNBIRDS.

Philepitta castanea (P.S. Müller)	AMNH (no number); Madagascar; 1929; Coll: Archbold-Rand Exp.
Neodrepanis corsuscans Sharpe	AMNH (no number); Madagascar; no other data.

FAMILY ACANTHISITTIDAE. NEW ZEALAND WRENS.

Acanthisitta chloris (Sparrman)	BM 1904-8-2; New Zealand; no other data.
Xenicus longipes (Gmelin)	BM 1940-12-8-89; New Zealand; Coll: Lord Rothschild.

SUBORDER MENURAE

FAMILY MENURIDAE. LYREBIRDS.

Menura novaehollandiae Latham, nestling	USNM 321461; Australia, New South Wales; 2 Aug 1931; Coll: K. A. Hindwood.

FAMILY ATRICHORNITHIDAE. SCRUB-BIRDS.

Atrichornis clamosus (Gould)	Nat. Mus. Victoria, R-11354; Albany, Western Australia; 25 Jan 1889; Coll: W. Webb.

APPENDIX B

SPECIES OF THE SUBORDER PASSERES EXAMINED

Listed below are the 534 species of oscines examined in this study. Most of the specimens were obtained from the same sources as the suboscines listed in Appendix A; a few were obtained from the Museum of Zoology, University of Michigan, Ann Arbor.

The order of families and family limits are those laid down by Wetmore (1960). Within each family the order and nomenclature of species follow the most recent revision, except as noted. For most families, the reference is the *Check-list of Birds of the World* (Mayr and Greenway, 1960, 1962; Mayr and Paynter, 1964; Paynter, 1967, 1968) or the *Catalogue of the Birds of the Americas* (Hellmayr, 1934-38). When neither of these sources has fully covered a family, I have compiled the list from the most recent regional works and have not cited them individually.

An exception to the above is the assemblage of New World nectar feeders sometimes grouped as the family Coerebidae. The compilers of the *Check-list of Birds of the World* have followed Beecher (1951) in dividing these birds between the Parulidae and Thraupidae, but Lowery and Monroe (in the *Check-list*)noted in their treatment of *Coereba* and *Conirostrum* (including *Atelodacnis*) that the former might warrant family status and the latter might belong in the family Emberizidae. Since my purpose in presenting this list is only to inform the reader of the species that I studied, and not to make taxonomic judgments, I am following Hellmayr (1935) for the Coerebidae.

FAMILY ALAUDIDAE. LARKS.

Ref: Peters, *in* Mayr and Greenway, 1960, p. 3–80.

Mirafra angolensis
Mirafra sabota
Melanocorypha yeltoniensis
Calandrella cinerea (4 specimens)
Calandrella rufescens
Galerida cristata (4 specimens)
Galerida modesta
Alauda arvensis
Eremophila alpestris

FAMILY HIRUNDINIDAE. SWALLOWS.

Ref: Peters, *in* Mayr and Greenway, 1960, p. 80–129.

Pseudochelidon eurystomina (4 specimens)
Pseudochelidon sirintarae
Tachycineta bicolor
Tachycineta albvienter
Tachycineta thalassina
Kalochelidon euchrysea
Progne tapera
Progne subis
Notiochelidon cyanoeuca
Stelgidopteryx ruficollis
Riparia paludicola
Riparia riparia (2 specimens)
Ptyonoprogne obsoleta
Hirundo rustica
Hirundo smithii
Petrochelidon pyrrhonota (2 specimens)
Delichon dasypus

FAMILY CAMPEPHAGIDAE. CUCKOO-SHRIKES.

Ref: Peters, Mayr and Deignan, *in* Mayr and Greenway, 1960, p. 167–221.

Coracina pectoralis
Coracina azurea
Coracina montana
Lalage maculosa
Campephaga phoenicea
Pericrocotus flammeus
Hemipus picatus
Terphrodornis pondicerianus

FAMILY DICRURIDAE. DRONGOS.

Ref: Vaurie, *in* Mayr and Greenway, 1962, p. 137–157.

Chaetorhynchus papuensis
Dicrurus aldabranus
Dicrurus hottentottus (2 specimens)
Dicrurus paradiseus (2 specimens)

FAMILY ORIOLIDAE. OLD WORLD ORIOLES.

Ref: Greenway, *in* Mayr and Greenway, 1962, p. 122–137.

Oriolus oriolus
Oriolus larvatus
Oriolus traillii
Sphecotheres flaviventris

FAMILY CORVIDAE. CROWS AND JAYS.

Ref: Blake and Vaurie, *in* Mayr and Greenway, 1962, p. 204–282.

Platyophus galericulatus
Cyanocitta cristata (3 specimens)
Aphelocoma coerulescens
Cyanocorax affinis
Cyanocorax yncas
Garrulus glandarius (2 specimens)
Perisoreus canadensis
Urocissa erythrorhyncha
Cissa chinensis
Cyanopica cyana
Dendrocitta occipitalis
Pica pica (2 specimens)
Nucifraga columbiana
Corvus brachyrhynchos (11 specimens)
Corvus corone
Corvus macrorhynchos
Corvus ruficollis
Corvus corax

FAMILY CRACTICIDAE. AUSTRALIAN MAGPIES.

Ref: Amadon, *in* Mayr and Greenway, 1962, p. 166–172.

Cracticus torquatus
Gymnorhina tibicen

FAMILY GRALLINIDAE. MUD-NEST BUILDERS.

Ref: Mayr, *in* Mayr and Greenway, 1962, p. 159–160.

Grallina cyanoleuca
Corcorax melanorhamphos

FAMILY PTILONORHYNCHIDAE. BOWERBIRDS.

Ref: Mayr, *in* Mayr and Greenway, 1962, p. 172–181.

Sericulus chrysocephalus
Ptilonorhynchus violaceus

FAMILY PARADISEIDAE. BIRDS OF PARADISE.

Ref: Mayr, *in* Mayr and Greenway, 1962, p. 181–204.

Manucodia sp.
Seleucidis melanoleuca

FAMILY SITTIDAE. NUTHATCHES.

Ref: Greenway, *in* Paynter, 1967, p. 125–149.

Sitta europaea (2 specimens)
Sitta pygmaea
Sitta krueperi
Sitta neumayer

Sitta pusilla
Sitta canadensis (2 specimens)
Sitta carolinensis
Sitta frontalis
Neositta chrysoptera (2 specimens)
Daphoenositta miranda

FAMILY PARIDAE. TITMICE. Ref: Snow, *in* Paynter, 1967, p. 52–124.

Aegothalos concinnus
Auriparus flaviceps
Parus artricapillus
Parus bicolor
Melanochlora sultanea

FAMILY HYPOSITTIDAE. CORAL-BILLED NUTHATCH. Ref: Greenway, *in* Paynter, 1967, p. 124.

Hypositta corallirostris

FAMILY CERTHIIDAE. CREEPERS. Ref: Greenway, *in* Paynter, 1967, p. 150–166.

Certhia familiaris (2 specimens)
Rhabdornis mysticalis
Climacteris rufa (3 specimens)

FAMILY CHAMAEIDAE. WRENTIT. Ref: Hellmayr, 1934.

Chamaea fasciata

FAMILY TIMALIIDAE. BABBLERS. Ref: Deignan, *in* Mayr and Paynter, 1964, p.228–442.

Orthonyx temminckii
Orthonyx spaldingii (2 specimens)
Psophodes olivaceus
Cinclosoma ajax
Ifrita kowaldi
Pellorneum ruficeps
Trichastoma tickelli
Pomatorhinus erythrogenys
Pomatorhinus ferruginosus
Neomixis tenella
Neomixis viridis
Stachyris pyrrhops
Stachyris nigriceps
Macronus flavicollis
Macronus gularis
Timalia pileata
Turdoides fulvus
Turdoides gymnogenys
Garrulax delesserti
Garrulax mitratus
Garrulax canorus
Leiothrix lutea
Minla cyanouroptera
Minla strigula
Heterophasia capistrata
Yuhina flavicollis
Yuhina gularis
Yuhina nigrimenta
Yuhina zantholeuca
Malia gratia
Oxylabes madagascariensis
Picathartes gymnocephalus

FAMILY PARADOXORNITHIDAE. PARROT-BILLS. Ref: Delacour, *in* Mayr and Greenway, 1960, p. 430–442.

Panurus biarmicus
Paradoxornis unicolor
Paradoxornis gularis

FAMILY PYCNONOTIDAE. BULBULS. Ref: Rand and Deignan, *in* Mayr and Greenway, 1960, p. 221–300.

Pycononotus jocosus
Pycnonotus barbatus
Pycnonotus virens
Pycnonotus latirostris
Pycnonotus tephrolaemus
Chlorocichla simplex
Phyllastrephus zosterops
Bleda syndactyla
Nicator chloris
Criniger calurus
Criniger flaveolus
Hypsipetes charlottae

Chlorocichla flavicollis
Phyllastrephus strepitans
Phyllastrephus madagascariensis
Hypsipetes mcclellandii
Hypsipetes virescens
Hypsipetes madagascariensis (2 specimens)

FAMILY CHLOROPSEIDAE. LEAFBIRDS.

Ref: Delacour, *in* Mayr and Greenway, 1960, p. 300–308.

Aegithina lafresnayi
Chloropsis cochinchinensis
Chloropsis hardwicki
Irena puella (2 specimens)

FAMILY CINCLIDAE. DIPPERS.

Ref: Greenway, *in* Mayr and Greenway, 1960, p. 374–379.

Cinclus cinclus
Cinclus mexicanus

FAMILY TROGLODYTIDAE. WRENS.

Ref: Paynter and Vaurie, *in* Mayr and Greenway, 1960, p. 379–440.

Campylorchynchus zonatus (3 specimens)
Cinnycerthia unirufa
Cistothorus palustris
Thryothorus atrogularis
Thryothorus rutilus
Thryothorus pleurostictus
Troglodytes aedon
Microcerculus marginatus (2 specimens)
Cyphorhinus aradus (2 specimens)

FAMILY MIMIDAE. MIMICS.

Ref: Davis and Miller, *in* Mayr and Greenway, 1960, p. 440–458.

Dumatella carolinensis
Melanoptila glabrirostris
Mimus polyglottos
Mimus gilvus
Mimodes graysoni
Oreoscoptes montanus
Toxostoma rufum
Cinclocerthia ruficauda
Donacobius atricapillus

FAMILY TURDIDAE. THRUSHES.

Ref: Ripley, *in* Mayr and Paynter, 1964, p. 13–227.

Brachypteryx montana
Erythropygia leucophrys
Erythropygia barbata
Pogonocichla stellata
Erithacus sharpei
Erithacus gunningi
Erithacus rubecula
Erithacus cyanurus
Phoenicurus phoenicurus
Phoenicurus frontalis
Phoenicurus auroreus
Cinclidium frontale
Sialia sialis
Sialia currucoides
Enicurus scouleri
Enicurus maculatus
Myadestes townsendi
Myadestes genibarbis (2 specimens)
Myadestes unicolor
Stizorhina fraseri
Cercomela familiaris
Saxicola rubetra
Saxicola torquata
Myrmecocichla arnotti (2 specimens)
Oenanthe isabellina
Cossypha natalensis
Cossypha niveicapilla
Cichladusa guttata
Alethe fuelleborni
Alethe montana
Copsychus saularis
Copsychus sechellarum
Copsychus malabaricus
Chaimarrornis leucocephalus
Saxicoloides fulicata
Monticola brevipes
Monticola solitarius
Myiophoneus caeruleus (2 specimens)
Zoothera naevia
Zoothera pinicola
Zoothera dauma
Catharus gracilirostris
Catharus occidentalis
Catharus fuscescens
Catharus minimus
Catharus ustulatus
Catharus guttatus
Hylocichla mustelina
Turdus litsipsirupa
Turdus plumbeus (2 specimens)

Oenanthe oenanthe (2 specimens)
Oenanthe deserti
Oenanthe hispanica
Oenanthe leucopyga
Oenanthe pileata
Turdus leucomelas
Turdus amaurochalinus
Turdus nudigenis
Turdus migratorius (4 specimens)

FAMILY ZELEDONIIDAE. WREN-THRUSH.

Ref: Ripley, *in* Paynter, 1964, p. 18.

Zeledonia coronata.

FAMILY SYLVIIDAE. OLD WORLD WARBLERS.

Ref: Regional works.

Tesia superciliosus
Cettia diphone
Cettia montana
Bradypterus castaneus
Bradypterus cinnamomeus (2 specimens)
Calamonastes fasciolatus
Melocichla mentalis
Cisticola chiniana
Cisticola cherrina
Cisticola brachyptera
Camaroptera brevicauda
Sylvietta brachyura
Prinia gracilis
Prinia atrogularis
Apalis flavida
Orthotomus astrogularis
Orthotomus cephium
Locustella ochotensis
Schoenicola brevirostris
Phragmaticola aëdon
Polioptila caerulea
Polioptila dumicola
Microbates cinereiventris
Rhamphocaenus melanurus
Lamprolia victoriae
Acrocephalus schoenobaenus
Acrocephalus scirpaceus
Acrocephalus caffra
Conopoderas familiaris
Cinclorhamphus cruralis
Hippolais icterinus
Hippolais pallida
Sylvia borin
Sylvia cantilans
Sylvia curruca
Sylvia melanocephala
Sylvia atricapilla
Phylloscopus sibilatrix
Phylloscopus coronatus
Phylloscopus trochilus
Seicercus ruficapilla
Seicercus burkei
Seicercus nouhuysei
Artisornis metopias
Abroscopus schistaceps
Hylia prasina
Malurus gouldi
Stipiturus malachurus
Gerygone flavolateralis
Sericornis magnirostris
Vitia ruficapilla

FAMILY REGULIDAE. KINGLETS.

Ref: Hellmayr, 1932.

Regulus calendula (2 specimens)
Regulus satrapa (2 specimens)

FAMILY MUSCICAPIDAE. OLD WORLD FLYCATCHERS.

Ref: Vaurie, 1953 (Muscicapinae); Paynter, 1967, p. 3–57 (Pachycephalinae); regional works (remainder).

Melaenornis chocolatina
Melaenornis edolioides
Melaenornis pammelaina
Ficedula hypoleuca
Ficedula albicollis
Ficedula monileger
Ficedula cyanomelaena
Niltava macgrigoriae
Niltava sundara
Niltava rubeculoides
Muscicapa striata
Tchitrea corvina
Erythrocercus mccalli
Monarcha alecto
Monarcha barbata
Monarcha axillaris
Monarcha guttula
Myiagra caledonica
Myiagra azureocapilla
Casiempis gayi
Arses telescophthalmus
Chelidorhynx hypoxanthura

Muscicapa sibirica
Muscicapa latirostris
Newtonia brunneicauda
Newtonia archboldi
Culicicapa ceylonensis
Pseudobias wardi
Diaphorophyia castanea
Batis minor
Trochocercus cyanomelas
Erranornis longicauda
Terpsiphone rufiventris
Petroica multicolor
Peneothello sigillata
Pachycephala pectoralis
Pachycephala schlegelii
Clytorhynchus pachycephaloides
Clytorhynchus nigrogularis
Peltops blainvillei
Pitohui dichrous
Rhipidura rufiventris
Rhipidura albolimbata
Rhipidura brachyrhynchus

FAMILY PRUNELLIDAE. ACCENTORS.

Ref: Ripley, *in* Mayr and Paynter, 1964, p. 3–12.

Prunella collaris (2 specimens)
Prunella montanella
Prunella modularis

FAMILY MOTACILLIDAE. WAGTAILS AND PIPITS.

Ref: Vaurie, White, Mayr and Greenway, *in* Mayr and Greenway, 1960, p. 129–167.

Motacilla flava
Motacilla cinerea (2 specimens)
Motacilla flaviventris
Anthus spinoletta

FAMILY BOMBYCILLIDAE. WAXWINGS.

Ref: Greenway, *in* Mayr and Greenway, 1960, p. 369–371.

Bombycilla garrulus
Bombycilla cedrorum

FAMILY PTILOGONATIDAE. SILKY FLYCATCHERS.

Ref: Greenway, *in* Mayr and Greenway, 1960, p. 371–373, 458.

Ptilogonys cinereus
Phainopepla nitens
Phainoptila melanoxantha

FAMILY DULIDAE. PALM CHAT.

Ref: Greenway, *in* Mayr and Greenway, 1960, p. 373–374.

Dulus dominicus (4 specimens)

FAMILY ARTAMIDAE. WOOD SWALLOWS.

Ref: Mayr, *in* Mayr and Greenway, 1962, p. 160–165.

Artamus leucorhynchus
Artamus maximus
Artamus cyanopterus

FAMILY VANGIDAE. VANGA SHRIKES.

Ref: Rand, *in* Mayr and Greenway, 1960, p.365–369.

Calicalicus madagascariensis
Schetba rufa
Vanga curvirostris
Falculea palliata
Leptopterus viridis
Leptopterus chabert
Leptopterus madagascarinus
Euryceros prevostii

FAMILY LANIIDAE. TYPICAL SHRIKES.

Ref: Rand, *in* Mayr and Greenway, 1960, p. 314–365.

Lanioturdus torquatus
Corvinella melanoleuca

Dryoscopus sabini
Tchagra minuta

Laniarius ferrugineus
Laniarius atrococcineus

FAMILY PRIONOPIDAE. HELMET SHRIKES.

Eurocephalus rüppelli
Eurocephalus anguitimens

FAMILY CYCLARHIDAE. PEPPERSHRIKES.

Cyclarhis gujanensis

FAMILY VIREOLANIIDAE. SHRIKE-VIREOS.

Vireolanius pulchellus

FAMILY CALLEIDAE. WATTLEBIRDS.

FAMILY STURNIDAE. STARLINGS.

Aplonis atrifusca
Aplonis tabuensis (2 specimens)
Aplonis opaca
Aplonis metallica
Onychognathus morio
Lamprotornis chloropterus
Lamprotornis acuticaudus
Cinnyricinclus sharpii
Cinnyricinclus leucogaster
Spreo superbus
Cosmopsarus unicolor
Saroglossa aurata

FAMILY MELIPHAGIDAE. HONEYEATERS.

Timeliopsis fulvigula
Lichmera indistincta
Myzomela nigrita
Meliphaga gracilis
Meliphaga fusca
Meliphaga subfrenata
Ptiloprora guisei

FAMILY NECTARINIIDAE. SUNBIRDS.

Anthreptes singalensis
Nectarinia asiatica

FAMILY DICAEIDAE. FLOWERPECKERS.

Melanocharis nigra
Dicaeum celebicum

Lanius cristatus
Lanius schach

Lanius nubicus
Pityriasis gymnocephala

Ref: Rand, *in* Mayr and Greenway, 1960, p. 309–314.

Prionops plumata
Prionops retzii
Prionops scopifrons

Ref: Blake, *in* Paynter, 1968, p. 103–108.

Ref: Blake, *in* Paynter, 1968, p. 108–110.

None examined.

Ref: Amadon, *in* Mayr and Greenway, 1962, p. 75–121.

Creatophora cinerea
Sturnus roseus
Sturnus vulgaris (2 specimens)
Sturnus contra (2 specimens)
Sturnus nigricollis
Acridotheres tristis
Acridotheres grandis
Mino dumontii
Sarcops calvus
Gracula religiosa
Scissirostrum dubium
Buphagus erythrorhynchus

Ref: Salomonsen, *in* Paynter, 1967, p. 338-450.

Melidectes princeps
Melidectes belfordi
Vosea whitemanensis
Moho braccatus
Acanthorhynchus tenuirostris
Promerops cafer

Ref: Rand, *in* Paynter, 1967, p. 208–289.

Arachnothera longirostra

Ref: Salomonsen, *in* Paynter, 1967, p. 166–208.

Dicaeum trochileum
Paramythia montium

FAMILY ZOSTEROPIDAE. WHITE-EYES.

Ref: Mayr and Moreau, *in* Paynter, 1967, p. 289–337.

Zosterops erythropleura
Zosterops lateralis
Zosterops montana
Woodfordia lacertosa
Chlorocharis emiliae
Zosterops senegalensis
Zosterops maderaspatana
Speirops lugubris

FAMILY VIREONIDAE. VIREOS.

Ref: Blake, *in* Paynter, 1968, p. 110–138.

Vireo griseus
Vireo nanus
Vireo olivaceus
Vireo gilvus
Hylophilus ochraceiceps

FAMILY COEREBIDAE. HONEYCREEPERS.

Ref: Hellmayr, 1935, Part 8, p. 218–331.

Coereba flaveola
Atelodacnis speciosa
Dacnis lineata
Euneornis campestris

FAMILY DREPANIDIDAE. HAWAIIAN HONEYCREEPERS.

Ref: Greenway, *in* Paynter, 1968, p. 93–103.

Himantione sanguinea
Vestiaria coccinea
Hemignathus obscurus
Hemignathus wilsoni
Viridonia virens
Psittirostra psittacea
Loxioides cantans

FAMILY PARULIDAE. NEW WORLD WARBLERS.

Ref: Lowery and Monroe, *in* Paynter, 1968, p. 3–82.

Mniotilta varia
Vermivora pinus
Dendroica caerulescens
Dendroica virens
Dendroica palmarum (2 specimens)
Dendroica striata
Dendroica castanea
Setophaga ruticilla
Seiurus aurocapillus
Helmintheros vermivorus
Prothonotaria citrea
Geothlypis agilis
Microligea palustris
Teretistris fornsi
Myioborus ornatus
Peucedramus olivaceus
Xenoligea montana
Granatellus venustus
Granatellus sallaei
Icteria virens

FAMILY PLOCEIDAE (INCLUDING ESTRILDIDAE). WEAVER-FINCHES AND WAXBILLS.

Ref: Moreau and Greenway, *in* Mayr and Greenway, 1962, p. 3–75; Mayr, *in* Paynter, 1968, p. 306–390.

Passer domesticus (8 specimens)
Euplectes orix
Chloebia gouldiae
Padda oryzivora

FAMILY ICTERIDAE. TROUPIALS.

Ref: Blake, *in* Paynter, 1968, p. 138–202.

Cacicus holocericeus
Icterus galbula
Agelaius phoeniceus (2 specimens)
Sturnella magna (3 specimens)
Sturnella neglecta
Quiscalus quiscula
Molothrus ater

FAMILY TERSINIDAE. SWALLOW TANAGER.

Ref: Hellmayr, 1936, part 9, p. 1–6.

Tersina viridis

FAMILY THRAUPIDAE. TANAGERS.

Ref: Hellmayr, 1936, p. 6–446.

Tanagra luteicapilla
Calospiza (= Tangara) cyanicollis
Calospiza (= Tangara) gyrola
Stephanophorus diadematus
Bangsia edwardsi
Thraupis episcopus (= virens)
Thraupis palmarum
Spindalis zena
Ramphocoelus icteronotus
Piranga olivacea (2 specimens)
Habia gutturalis (2 specimens)
Rhodinocichla rosea
Calyptophilus frugivorus
Hemithraupis guira
Nesospingus speculiferus
Schistochlamys melanops

FAMILY FRINGILLIDAE. SPARROWS AND BUNTINGS.

Ref: Hellmayr, 1938, Part 11, 662 p.; Howell and Paynter, *in* Paynter, 1968, p. 207–306.

Saltator albicollis
Gubernatrix cristata
Paroaria coronata
Richmondena cardinalis
Hedymeles ludovicianus
Hedymeles melanocephalus
Passerina cyanea (2 specimens)
Fringilla coelebs
Montifringilla nivalis
Pinaroloxias inornatus
Carduelis chloris
Carduelis pinus
Carduelis carduelis
Acanthis flammea
Carpodacus purpureus
Pinicola enucleator
Loxia curvirostra
Coccothraustes vespertinus
Loxigilla violacea
Sporophila minuta
Volatinia jacarina
Sicalis lebruni
Diuca diuca
Phrygilus patagonicus
Phrygilus gayi
Phrygilus fruticeti
Phrygilus carbonarius
Melanodera melanodera
Coryphospingus cucullatus
Atlapetes albofrenatus
Arremon aurantiirostris
Arremonops conirostris
Piplio erythrophthalmus
Myiospiza humeralis
Passerculus sandwichensis
Ammodramus savannarum
Ammospiza caudacuta
Ammospiza maritima
Chondestes grammacus
Aimophila strigiceps
Amphispiza bilineata
Junco hyemalis
Junco oreganus
Spizella pusilla
Zonotrichia albicollis
Zonotrichia capensis
Passerella iliaca
Melospiza melodia (2 specimens)
Emberizoides herbicola
Poospiza torquata (2 specimens)
Saltricula multicolor
Embernagra platensis
Calcarius lapponicus (4 specimens)
Plectrophenax nivalis
Emberiza melanocephala

INDEX

This index is intended to provide the reader with reference to morphological descriptions and taxonomic discussion only. The pages indicated in Roman type contain morphological descriptions; those in italics contain taxonomic discussion. The two page references (which may be the same) following the generic name locate descriptions of syringeal cartilages and musculature, respectively. If one of these aspects of the syrinx is not described, a dash is provided in order to identify the single page reference.

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PLATES

The following plates represent the majority of syringeal variations encountered in this study. To facilitate comparisons, all syringes are shown at about the same size, instead of to the same scale. The figures therefore represent various magnifications of the actual syringes rounded to the nearest integer. Where great variability exists among the specimens of a species, the specimen number of the individual drawn is indicated in the relevant caption. Where no number is given, either the species is uniform in structure, or only a single individual was examined.

In all the plates the stippled areas represent bone or cartilage, with no attempt to differentiate between various cartilage tissue types. Clear areas within each figure are membranous or, when continuous with muscle (as in *Legatus*, Pl. 8), tendinous.

PLATE 1

Nomenclature

FIG. 1 Configurations of cartilaginous elements.

FIG. 2 Oblique views and sections of the right halves of typical divided A- and B-elements.

FIG. 3 Simplified tracheobronchial junction in ventrilateral view, showing extrinsic syringeal muscles: M. sternotrachealis and M. tracheolateralis.

FIG. 4 Same, showing only M. obliquus ventralis.

FIG. 5 Same, showing M. obliquus lateralis; M. obliquus ventralis cut away.

FIG. 6 Simplified tracheobronchial junction, dorsolateral view, showing M. obliquus dorsalis, internal tympaniform membrane, and internal cartilage.

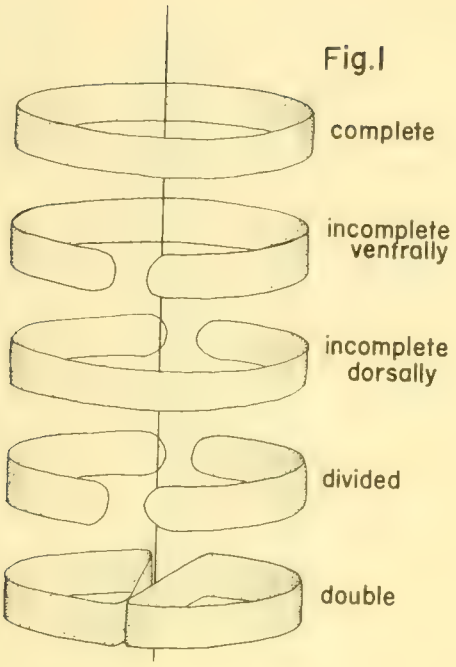


Fig.1

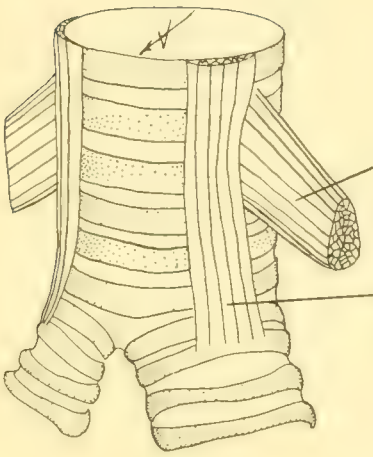


Fig.3

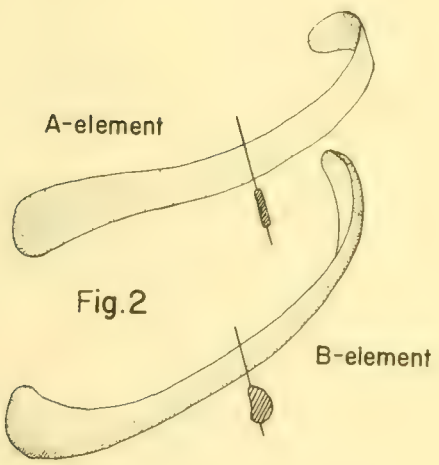


Fig.2

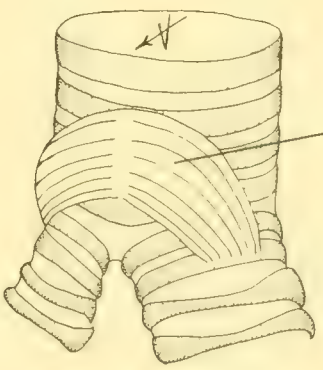


Fig.4

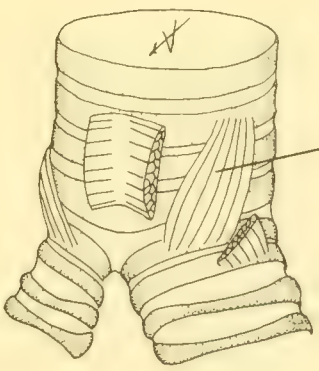


Fig.5

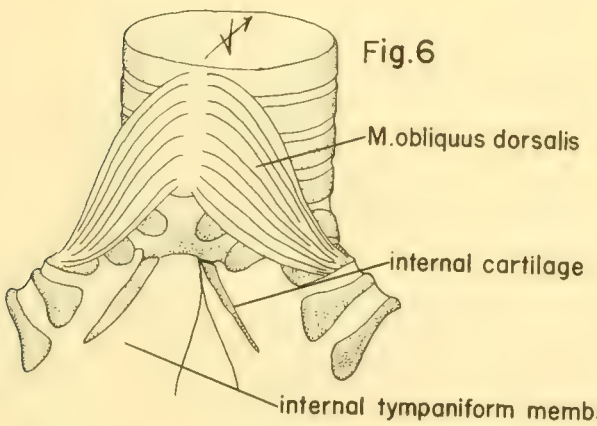


Fig.6

PLATE 2

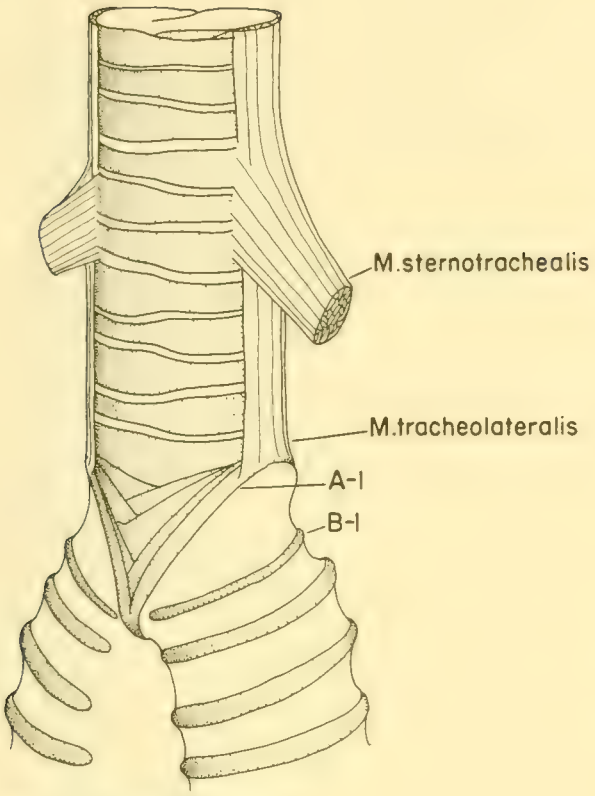
Eurylaimidae

Psarisomus dalhousei, ventrilateral view, ×8.

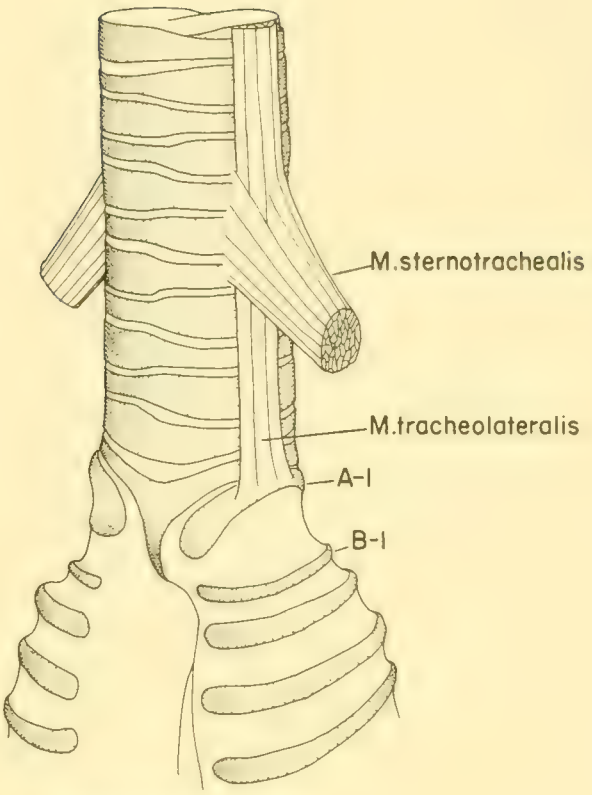
Same, dorsolateral view, ×8.

Calyptomena whiteheadi, ventrilateral view, ×5.

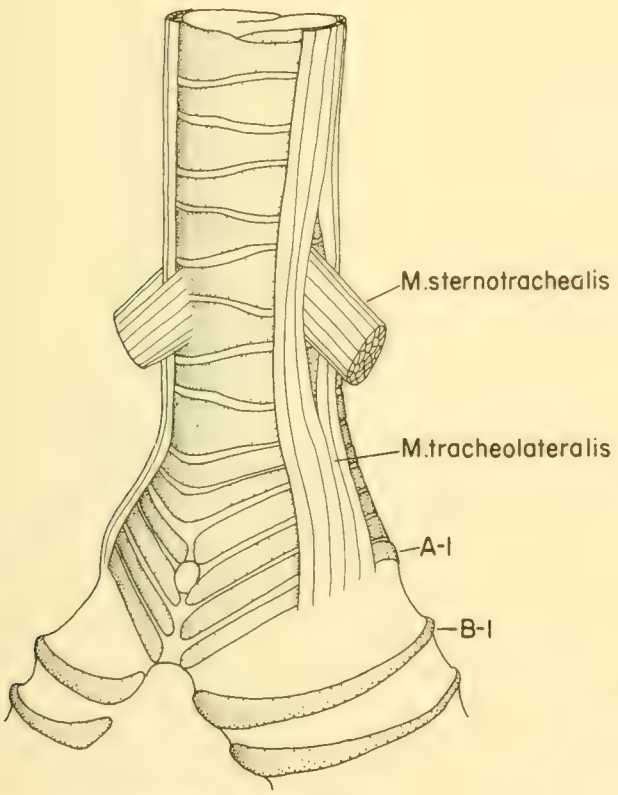
Same, dorsolateral view, ×5.



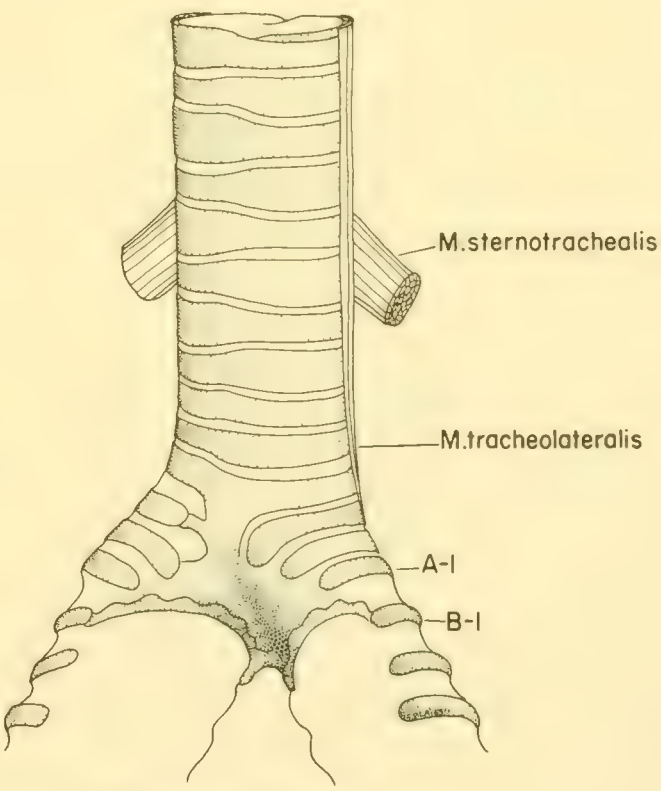
Psarisomus, ventral



Psarisomus, dorsal



Calyptomena, ventral



Calyptomena, dorsal

PLATE 3

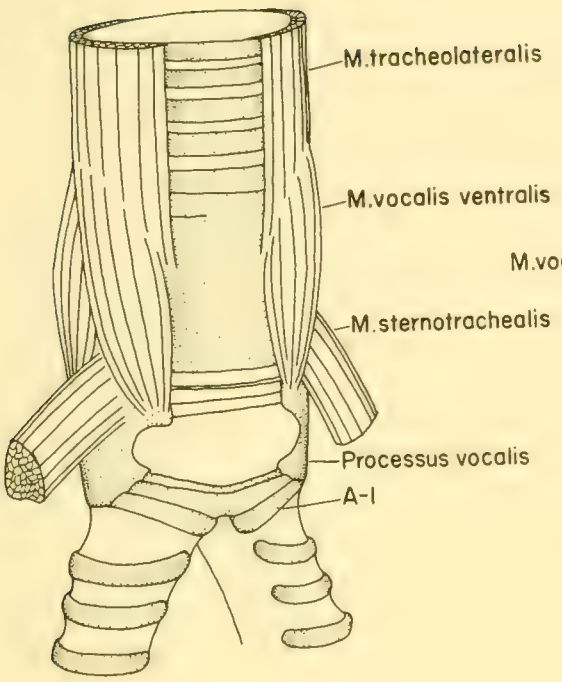
Furnarioidea (I)

Campylorhamphus trochilirostris, (Dendrocolaptidae), ventrilateral view, ×6.

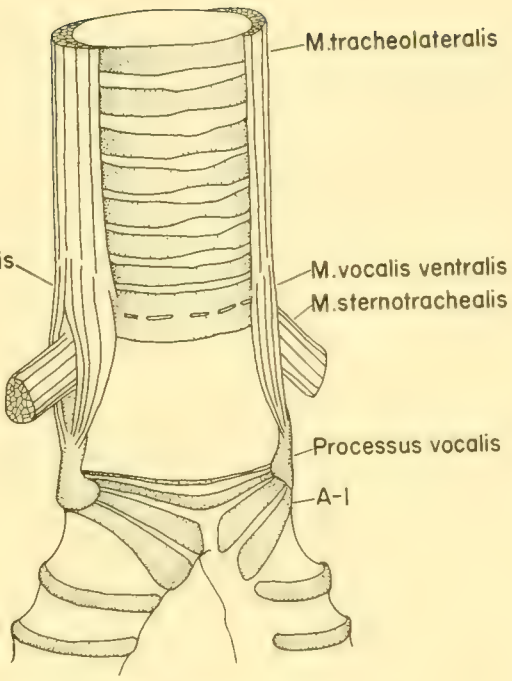
Cinclodes fuscus (Furnariidae), ventrilateral view, ×6.

Taraba major (Formicariidae), ventrilateral view, ×6.

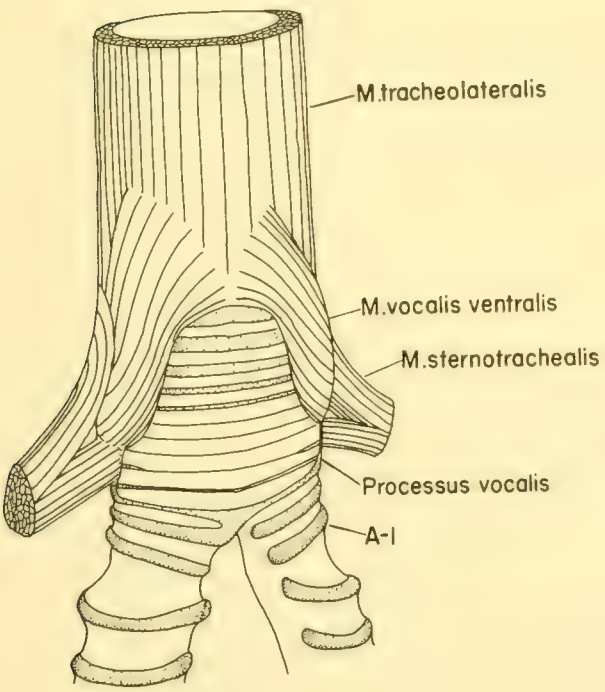
Formicarius analis (Formicariidae), ventrilateral view, ×6.



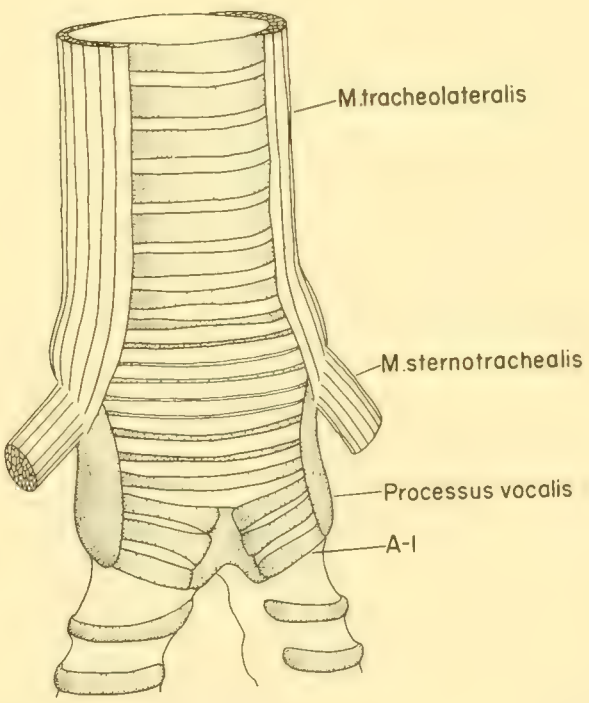
Campylorhamphus



Cinclodes



Taraba



Formicarius

PLATE 4

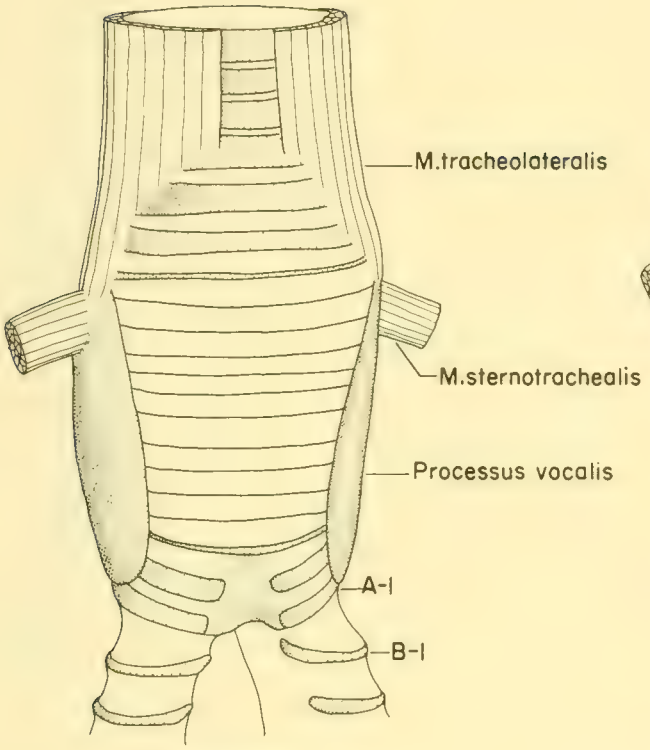
Furnarioidea (II)

Chamaeza brevicauda (Formicariidae), ventrilateral view, ×6.

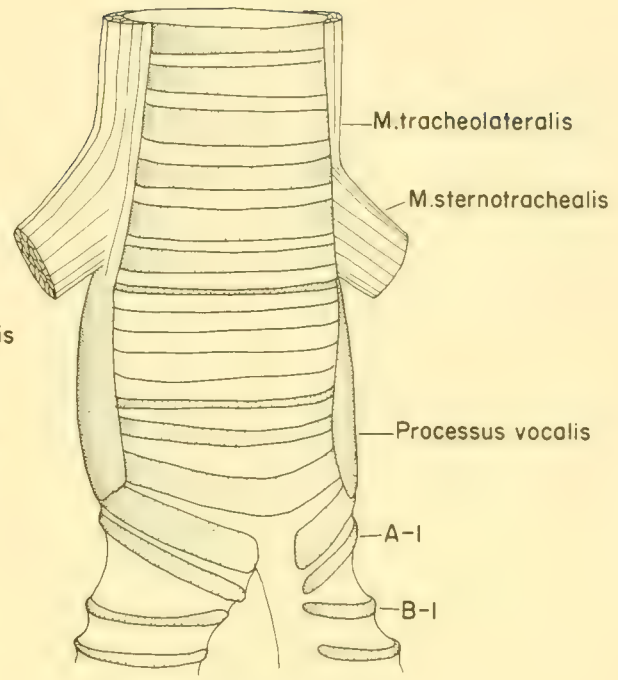
Conopophaga roberti (Formicariidae), ventrilateral view, ×8.

Melanopareia maximilliani (Rhinocryptidae), ventrilateral view, ×6.

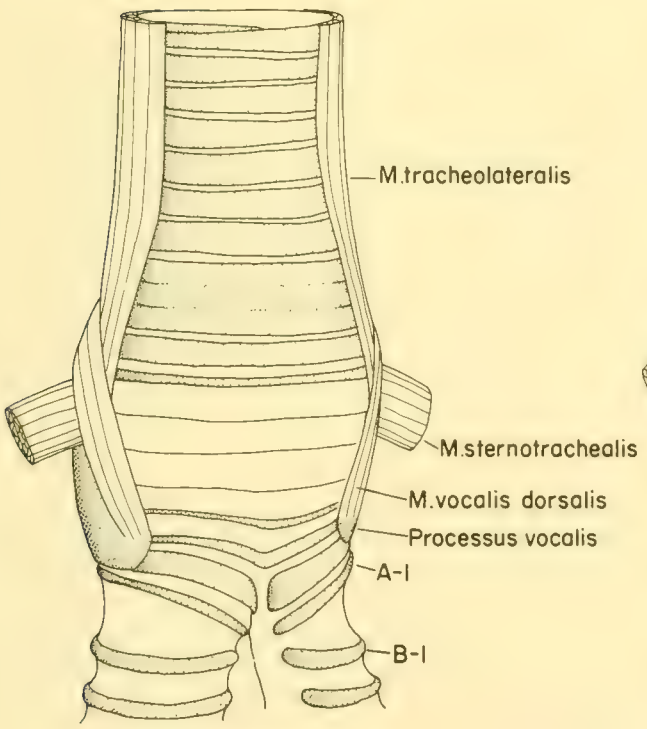
Pteroptochos tarnii (Rhinocryptidae), ventrilateral view, ×5.



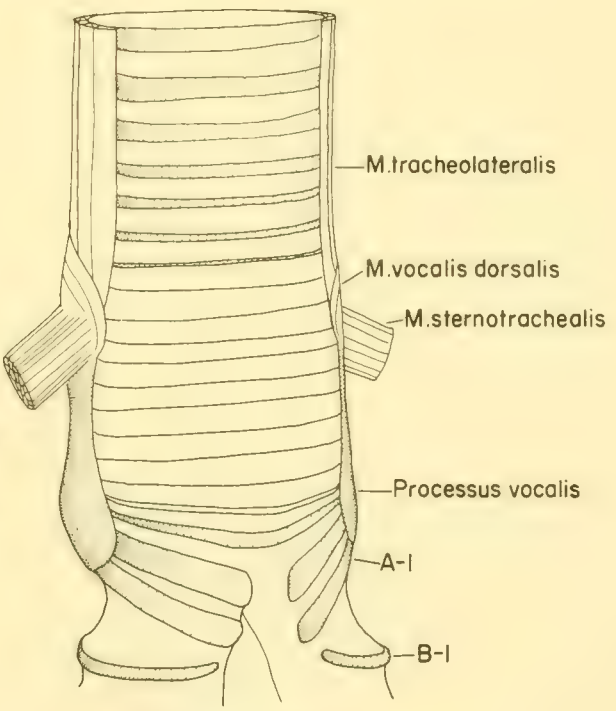
Chamaeza



Conopophaga



Melanopareia



Pteroptochos

PLATE 5

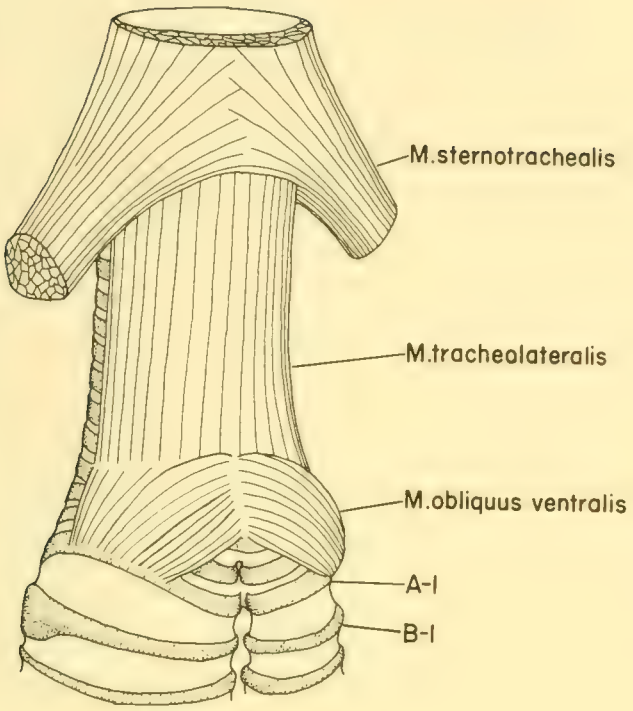
Tyrannidae (I), Ventral

Xolmis irupero, ventrilateral view, ×5.

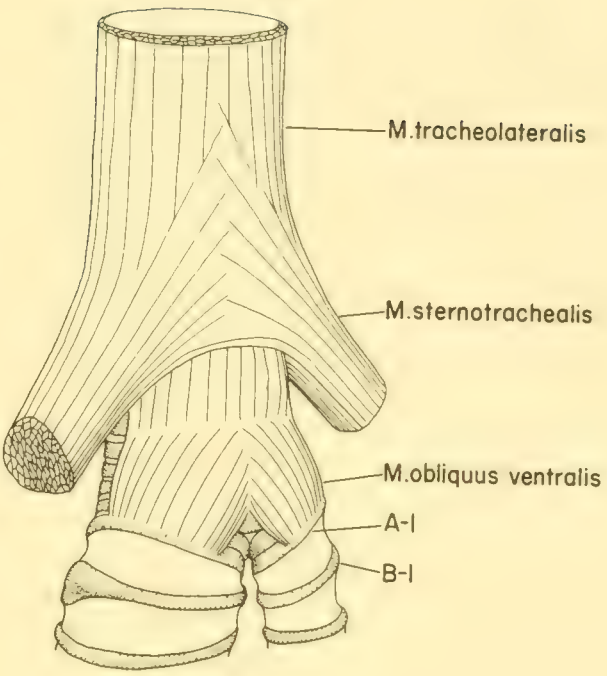
Lessonia rufa, ventrilateral view, ×9.

Sayornis phoebe, ventrilateral view, ×6.

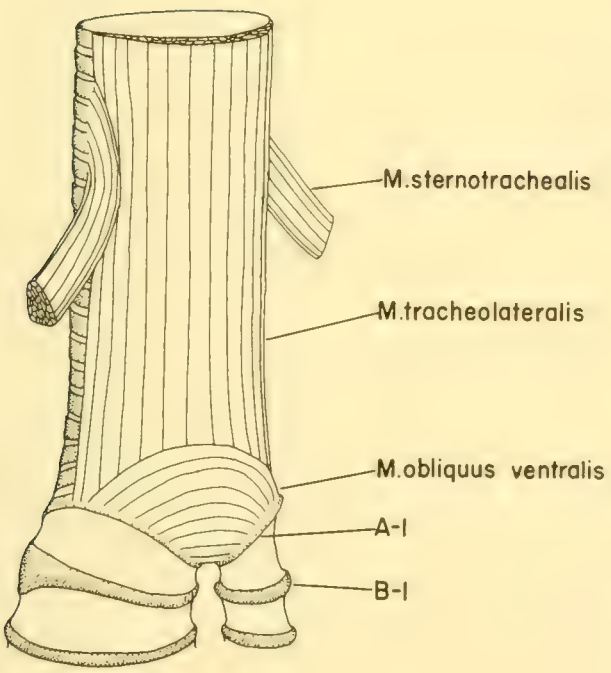
Colonia colonus (YPM 2634), ventrilateral view, ×8.



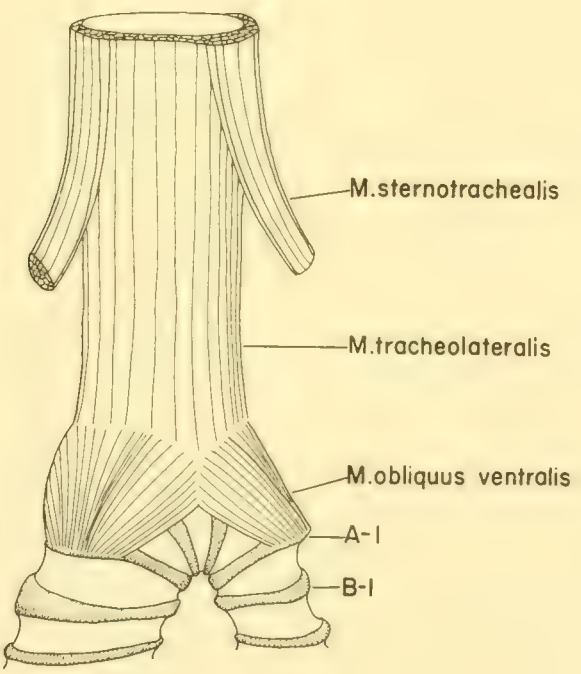
Xolmis



Lessonia



Sayornis



Colonia

PLATE 6

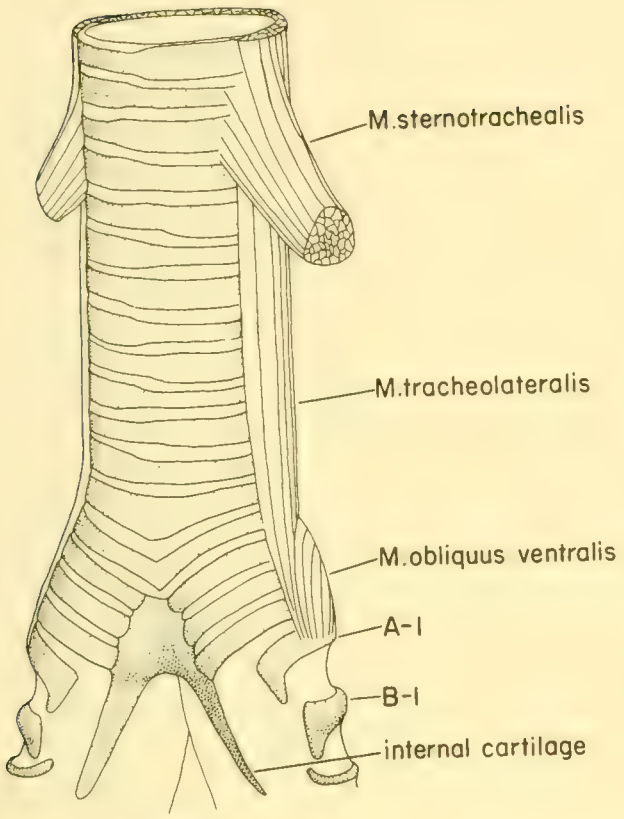
Tyrannidae (I), Dorsal

Xolmis irupero, dorsolateral view, ×5.

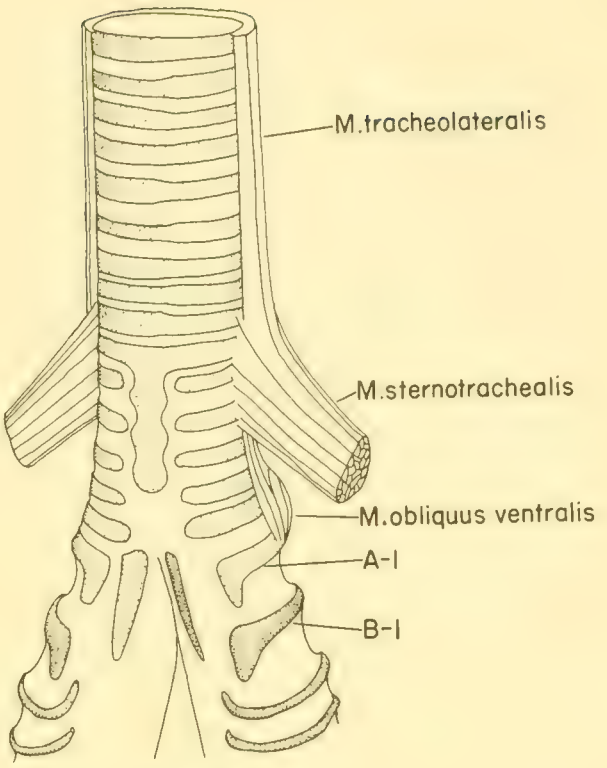
Lessonia rufa, dorsolateral view, ×9.

Sayornis phoebe, dorsolateral view, ×6.

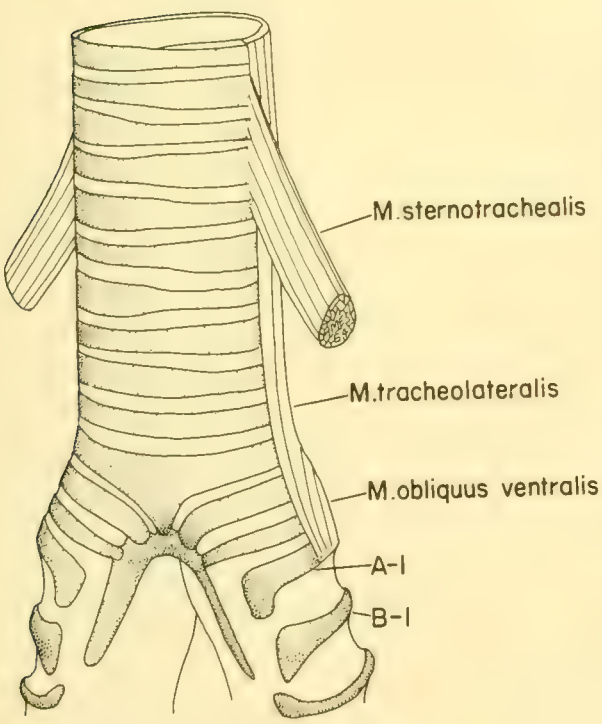
Colonia colonus (YPM 2634), dorsolateral view, ×8.



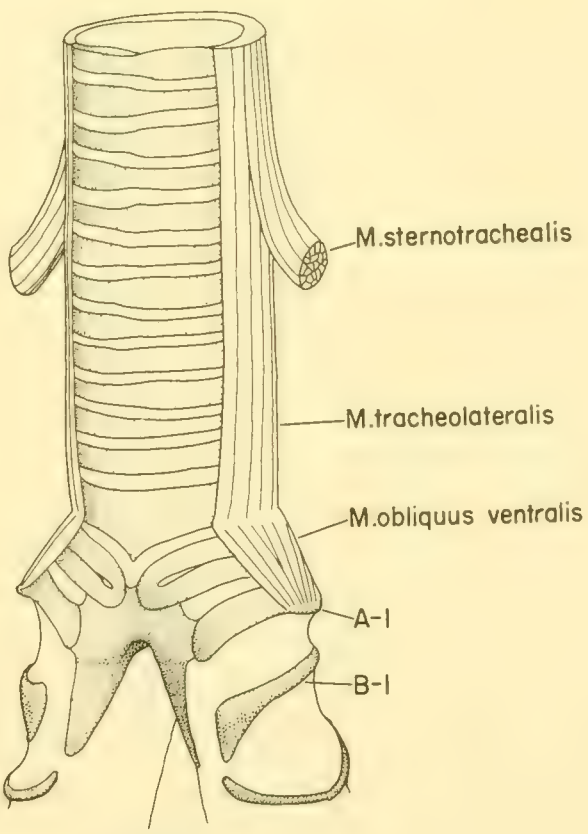
Xolmis



Lessonia



Sayornis



Colonia

PLATE 7

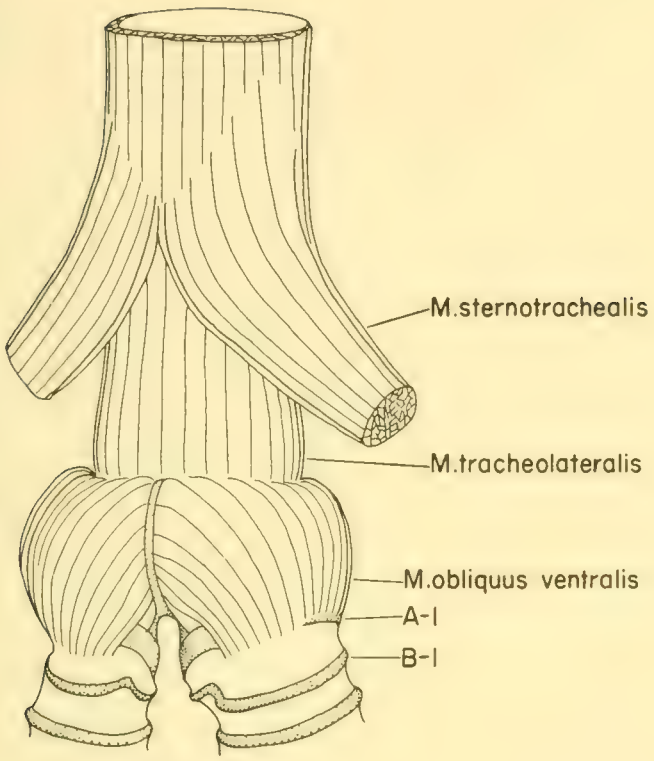
Tyrannidae (II), Ventral

Lichenops perspicillata, ventrilateral view, ×5.

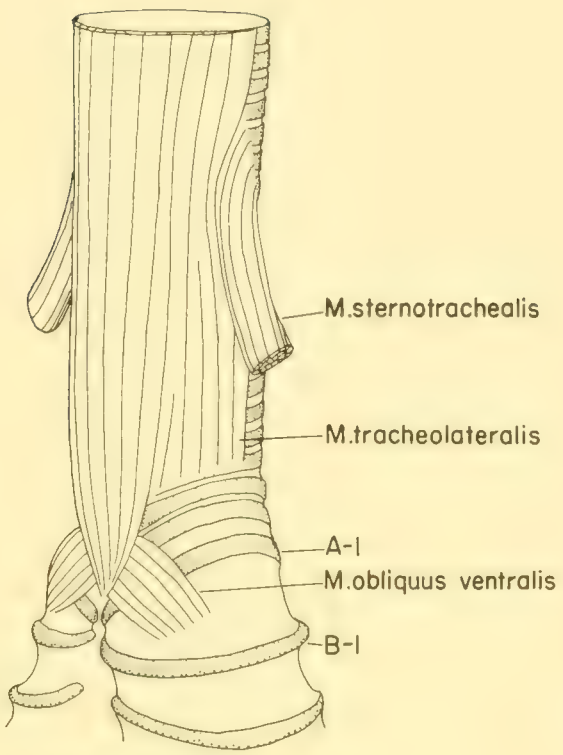
Pyrocephalus rubinus (YPM 2177), ventrilateral view, ×6.

Machetornis rixosa, ventrilateral view, ×5.

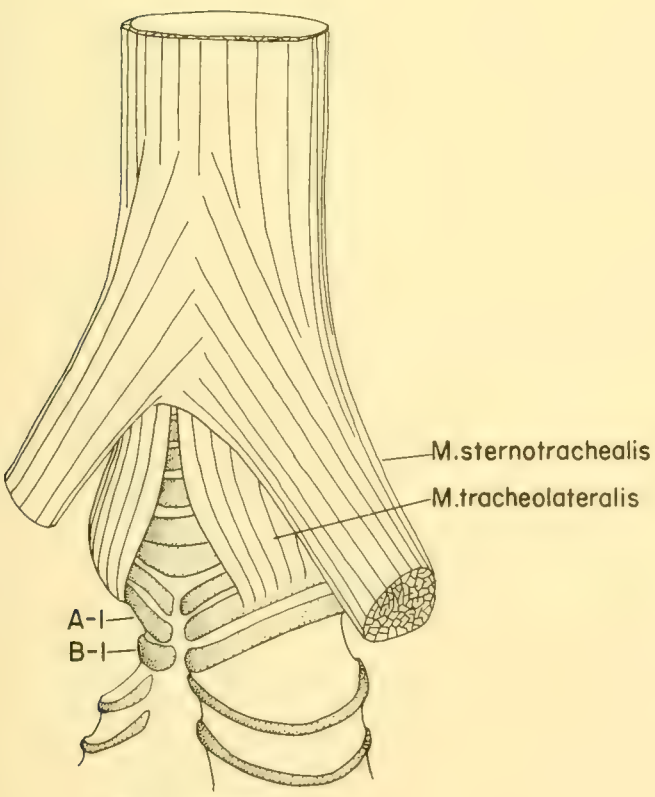
Legatus leucophaius, ventrilateral view, ×6.



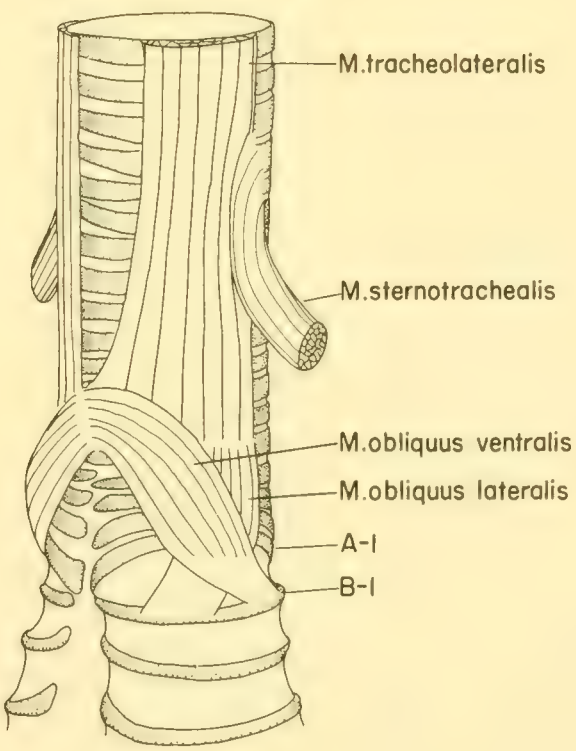
Lichenops



Pyrocephalus



Machetornis



Legatus

PLATE 8

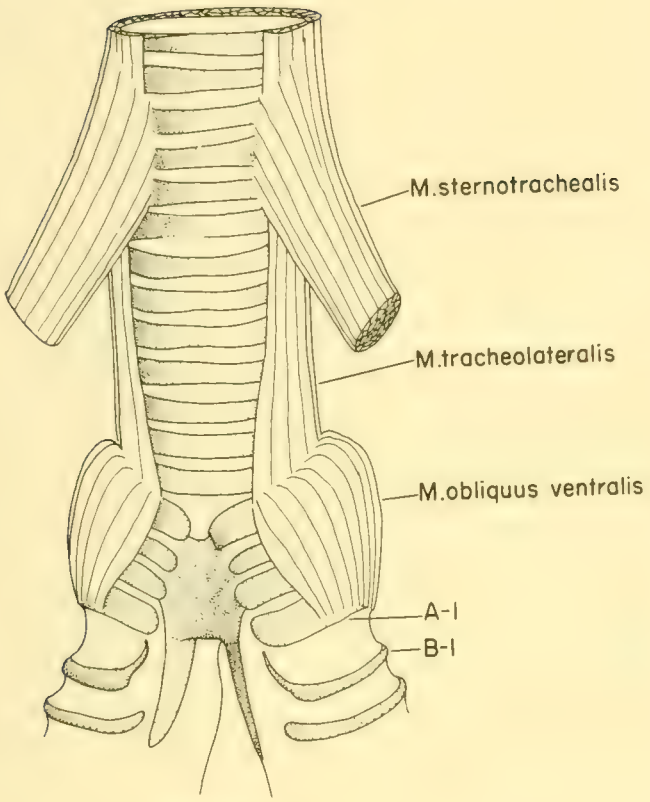
Tyrannidae (II), Dorsal

Lichenops perspicillata, dorsolateral view, ×5.

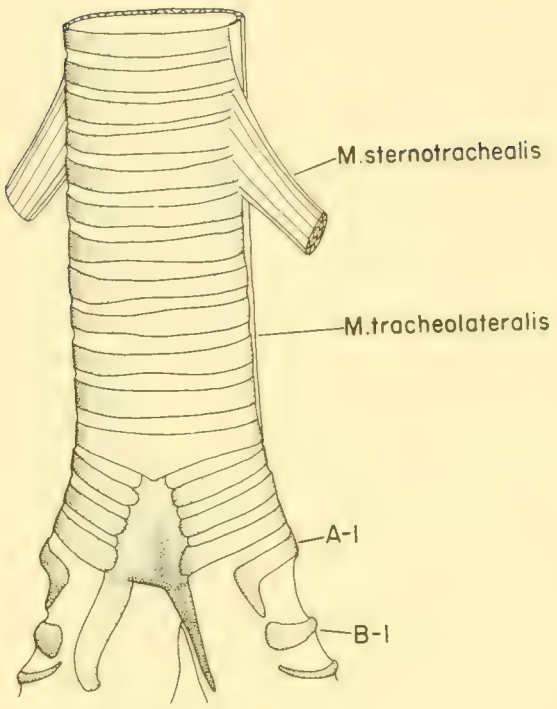
Pyrocephalus rubinus (YPM 2177), dorsolateral view, ×6.

Machetornis rixosa, dorsolateral view, ×5.

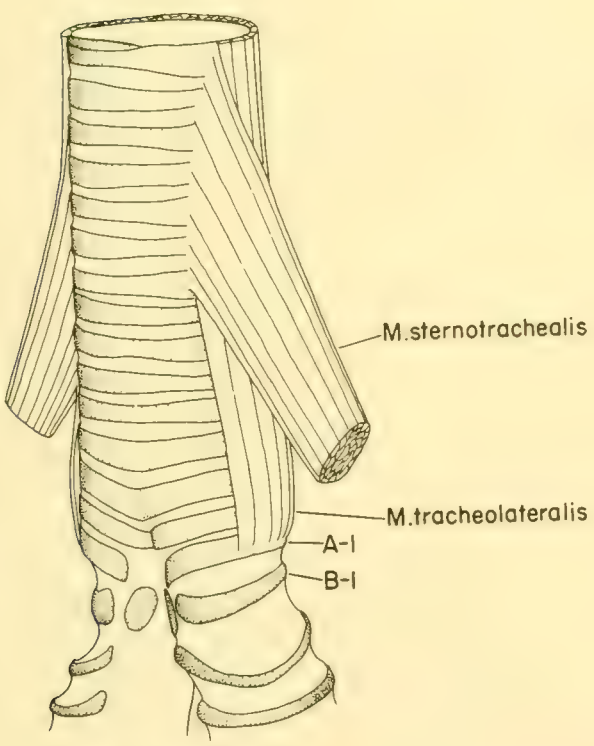
Legatus leucophaius, dorsolateral view, ×5.



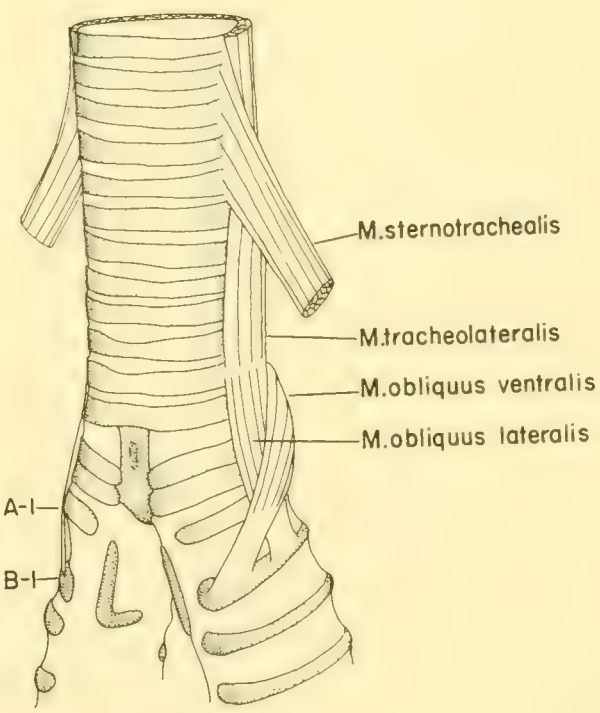
Lichenops



Pyrocephalus



Machetornis



Legatus

PLATE 9

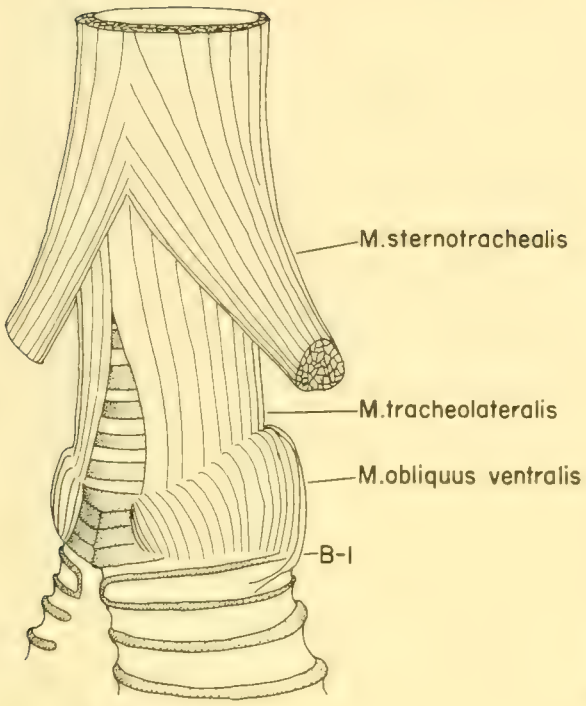
Tyrannidae (III), Ventral

Tyrannus tyrannus (YPM 706), ventrilateral view, ×5.

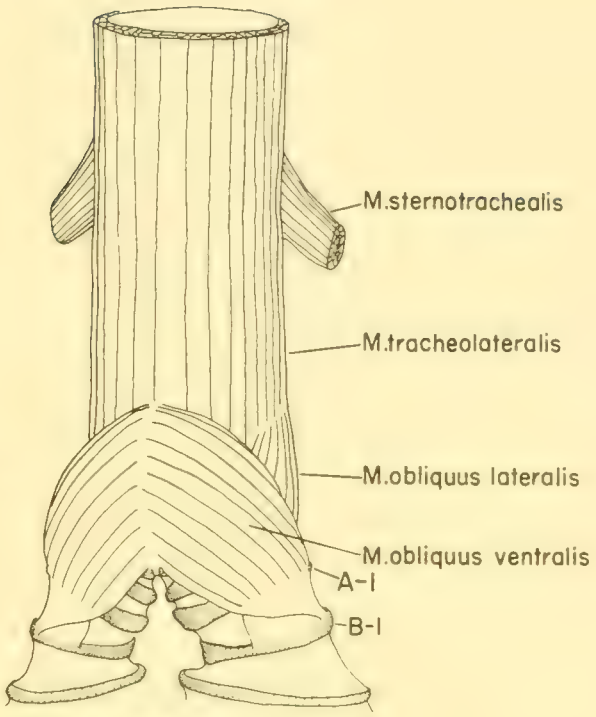
Myiozetetes similis (YPM 1543), ventrilateral view, ×7.

Myiarchus crinitus (YPM 759), ventrilateral view, ×5.

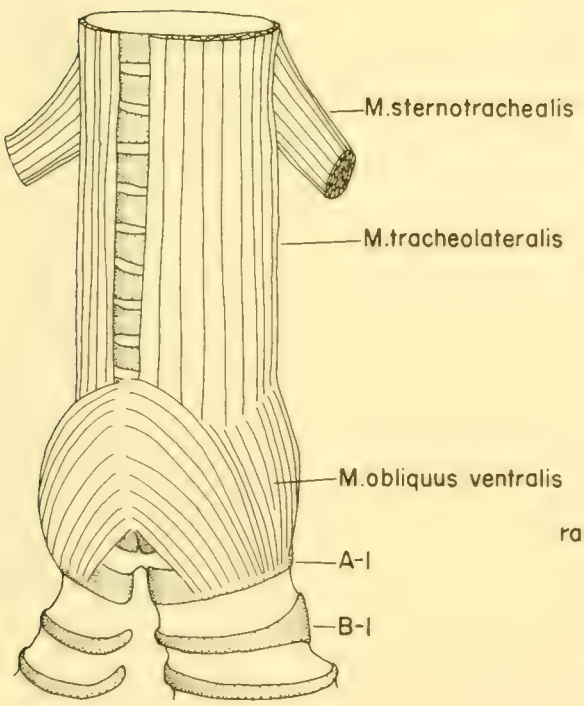
Nuttallornis mesoleucus, ventrilateral view, ×6.



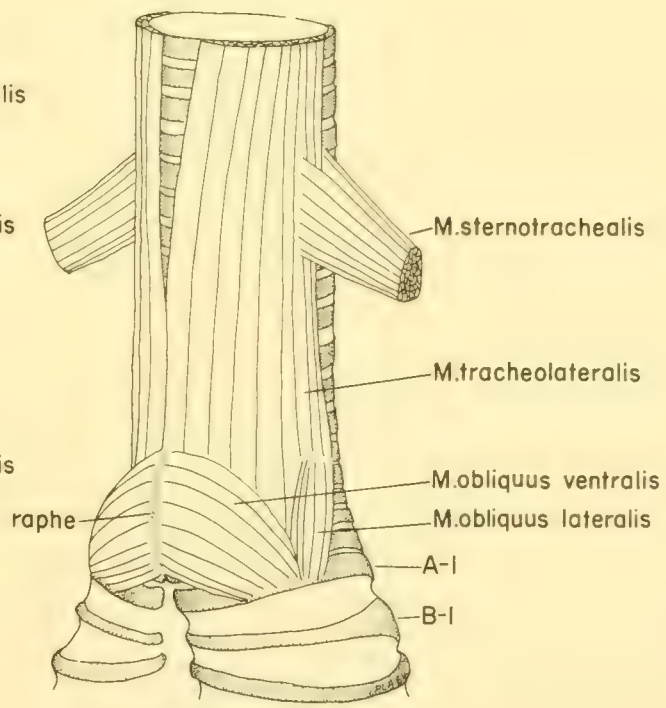
Tyrannus



Myiozetetes



Myiarchus



Nuttallornis

PLATE 10

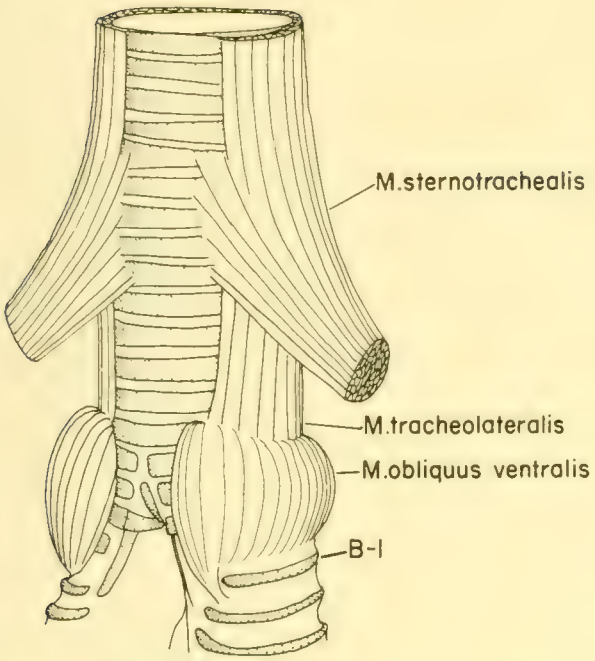
Tyrannidae (III), Dorsal

Tyrannus tyrannus (YPM 706), dorsolateral view, ×5.

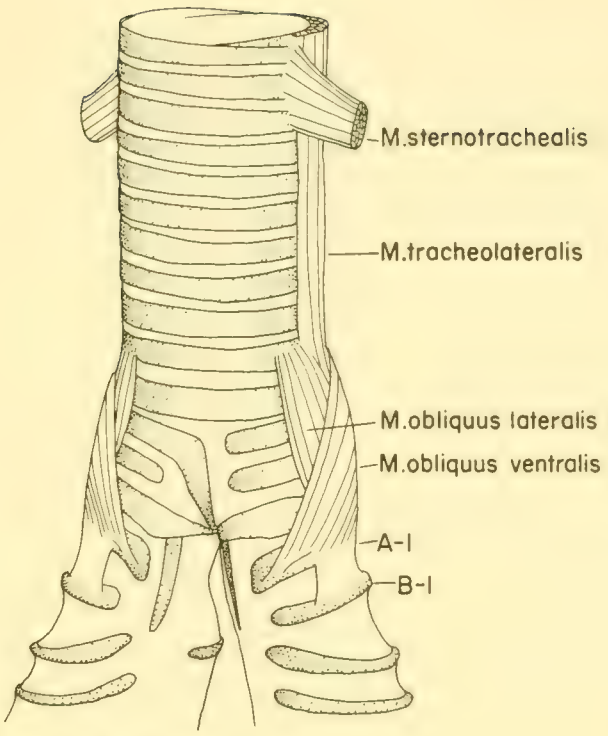
Myiozetetes similis (YPM 1543), dorsolateral view, ×7.

Myiarchus crinitus (YPM 759), dorsolateral view, ×5.

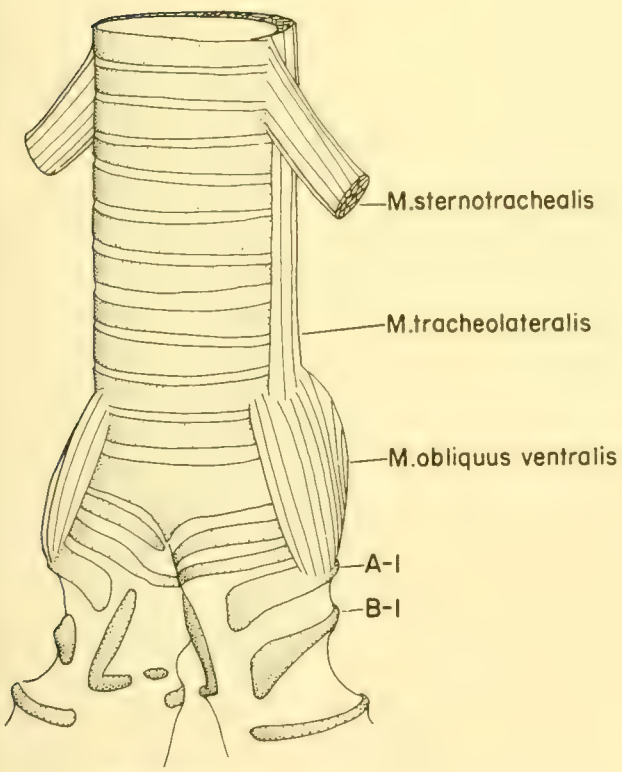
Nuttallornis mesoleucus, dorsolateral view, ×6.



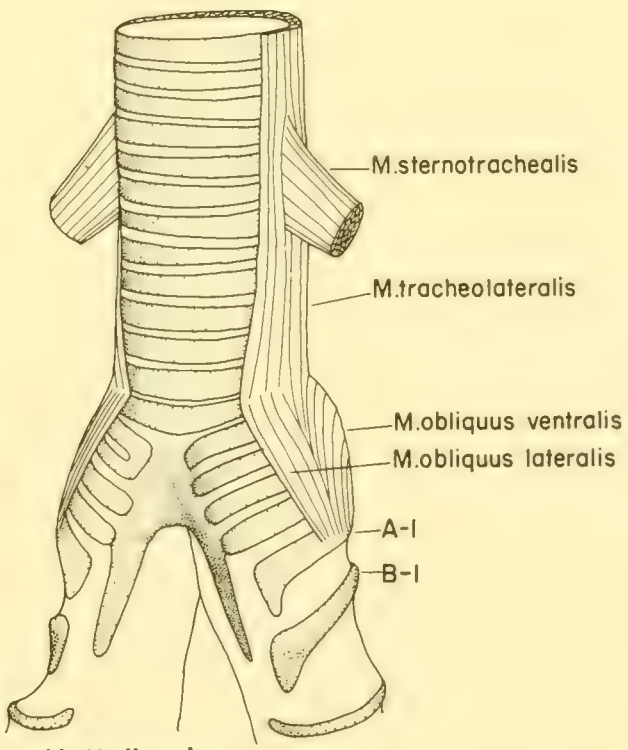
Tyrannus



Myiozetetes



Myiarchus



Nuttallornis

PLATE 11

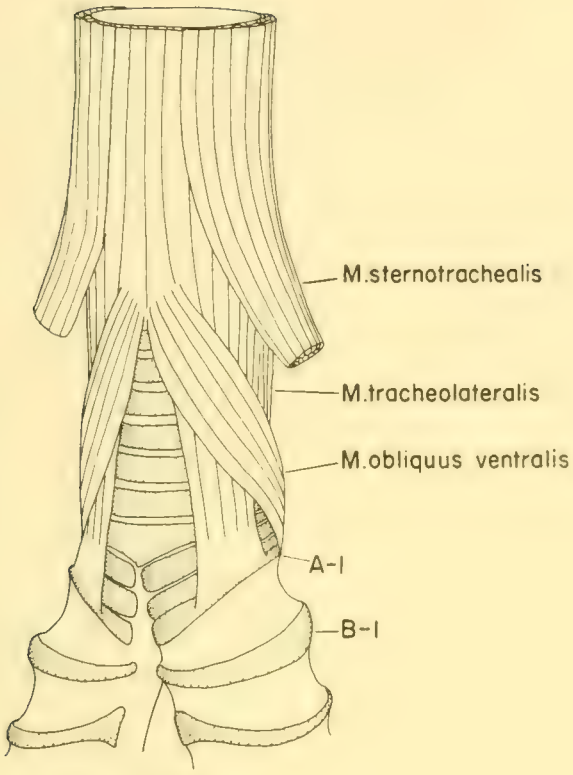
Tyrannidae (IV), Ventral

Platyrinchus mystaceus, ventrilateral view, ×12.

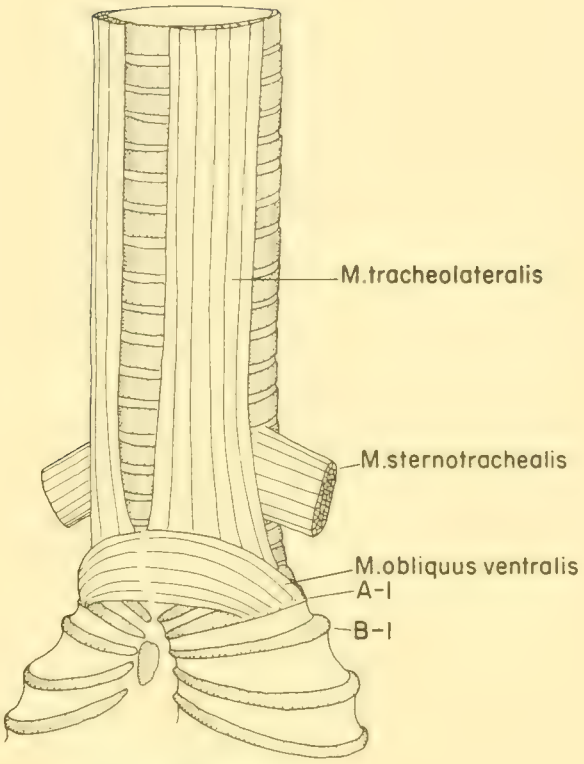
Rhynchocyclus brevirostris, ventrilateral view, ×9.

Todirostrum sylvia (YPM 1763), ventrilateral view, ×12.

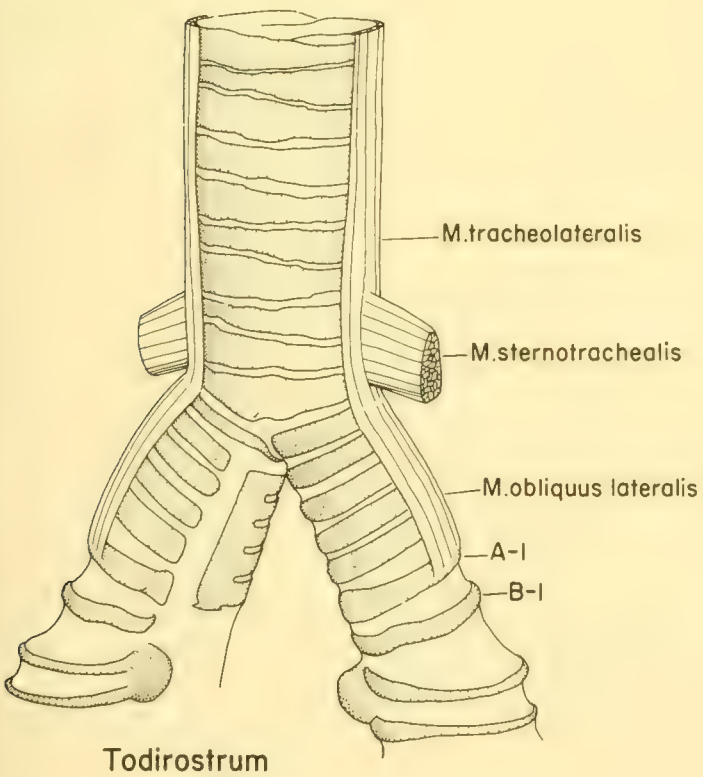
Terenotriccus erythrurus, ventrilateral view, ×12.



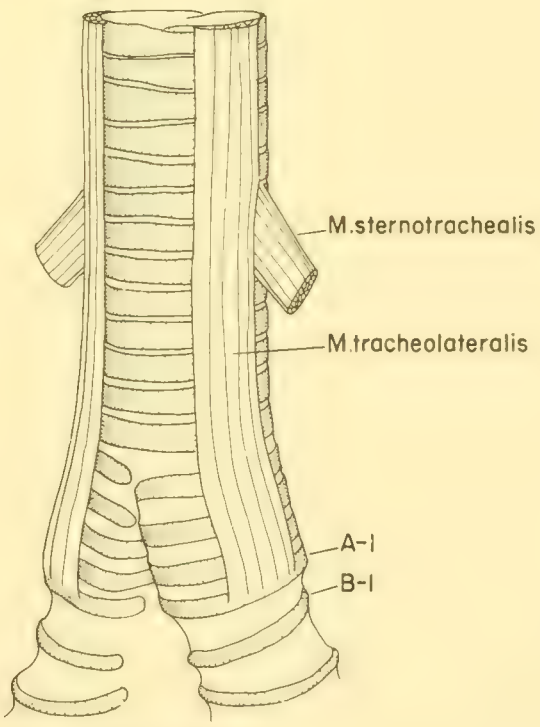
Platyrinchus



Rhynchocyclus



Todirostrum



Terenotriccus

PLATE 12

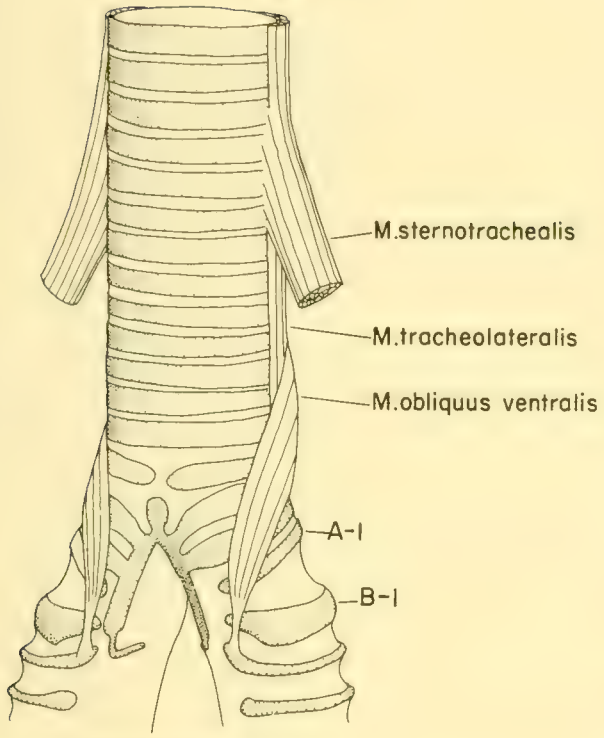
Tyrannidae (IV), Dorsal

Platyrinchus mystaceus, dorsolateral view, ×12.

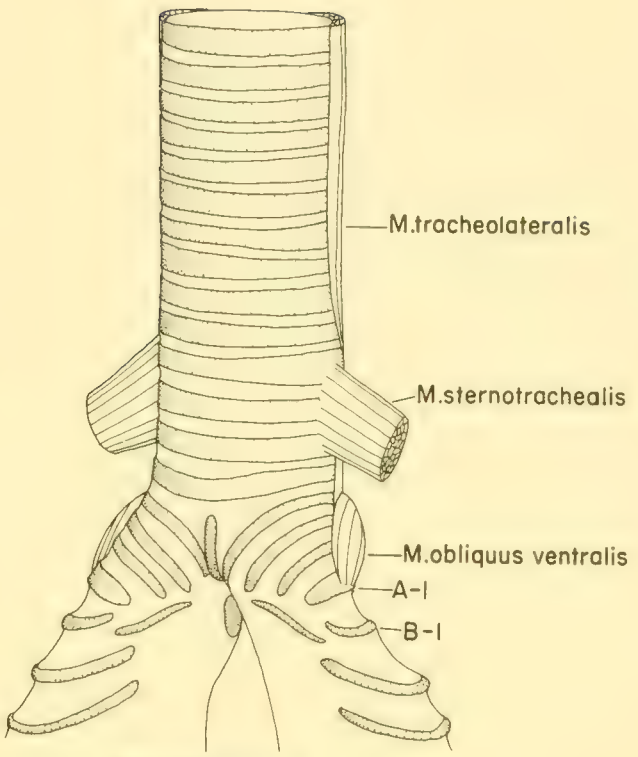
Rhynchocyclus brevirostris, dorsolateral view, ×9.

Todirostrum sylvia (YPM 1763), dorsolateral view, ×12.

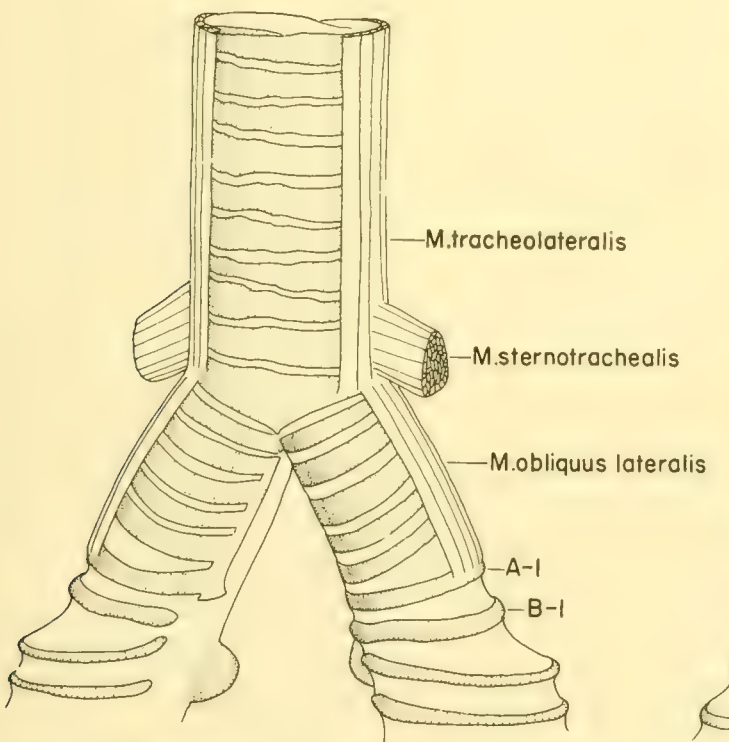
Terenotriccus erythrurus, dorsolateral view, ×12.



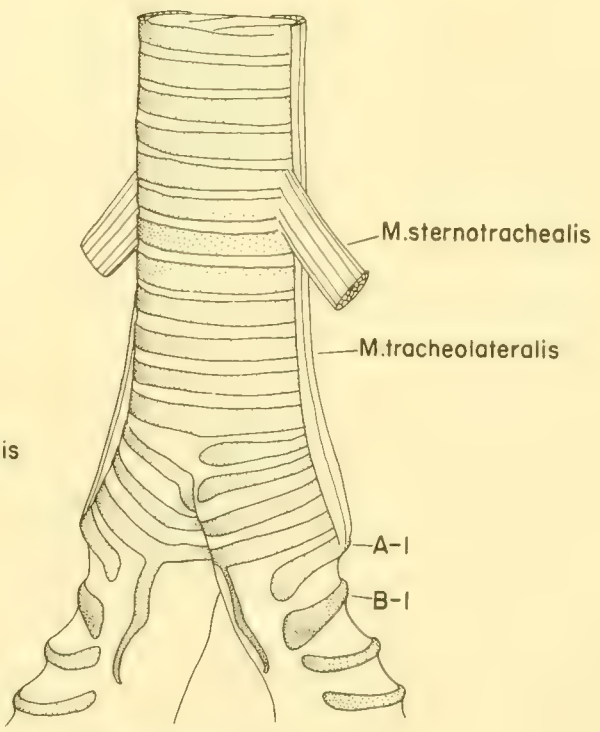
Platyrinchus



Rhynchocyclus



Todirostrum



Terenotriccus

PLATE 13

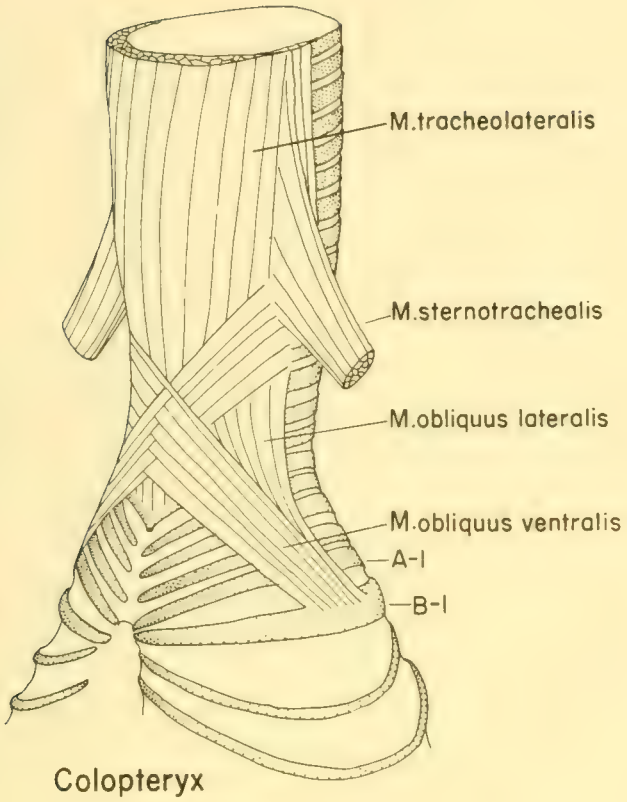
Tyrannidae (V), Ventral

Colopteryx galeata, ventrilateral view, ×12.

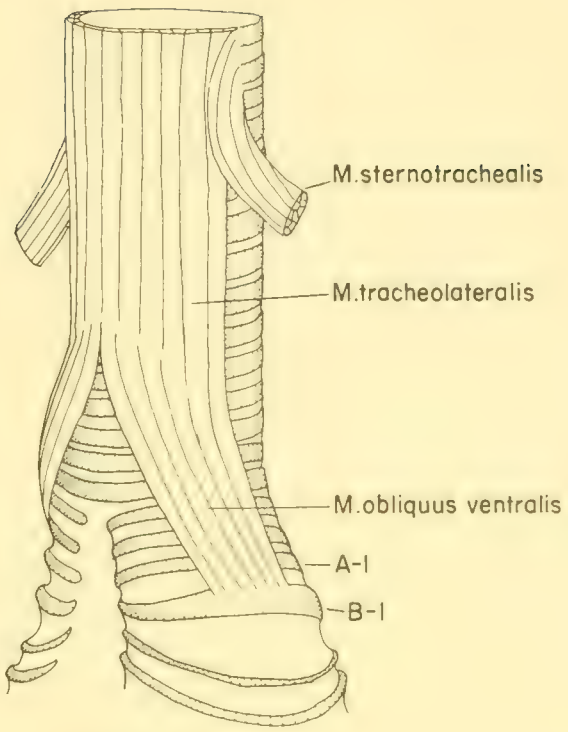
Tachuris rubrigastra, ventrilateral view, ×14.

Elaenia viridicata, ventrilateral view, ×8.

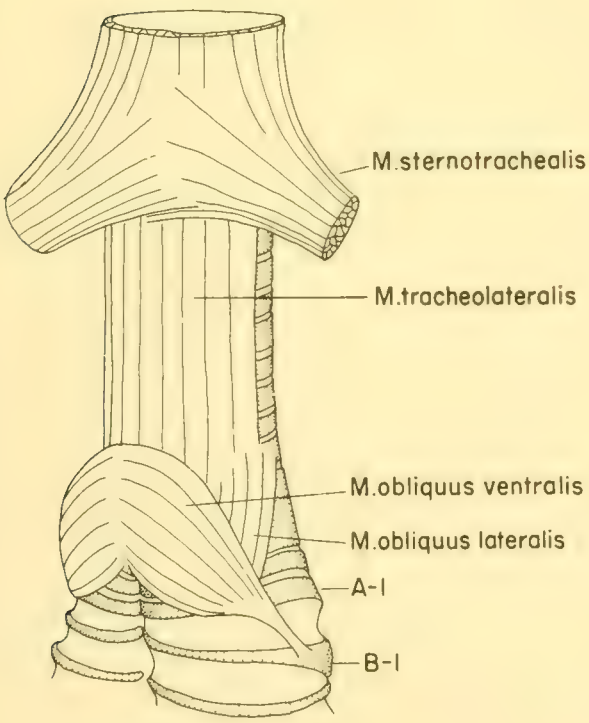
Pipromorpha oleaginea, ventrilateral view, ×9.



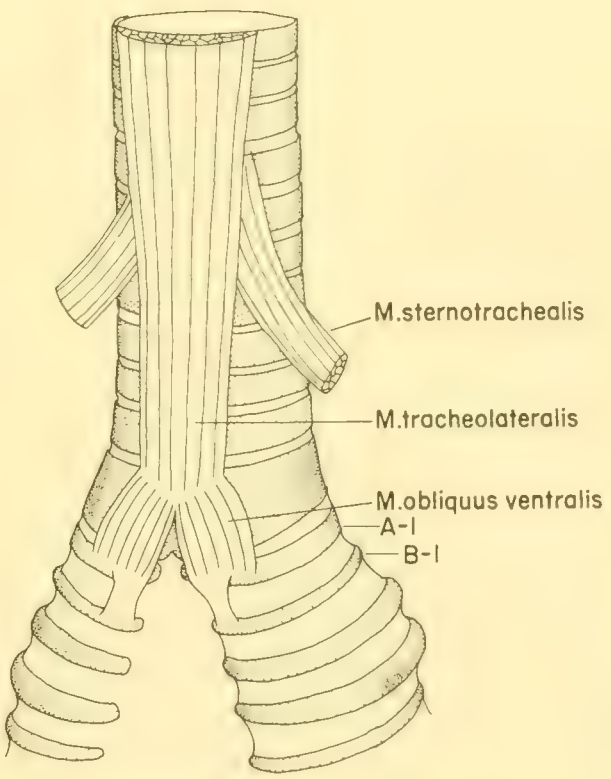
Colopteryx



Tachuris



Elaenia



Pipromorpha

PLATE 14

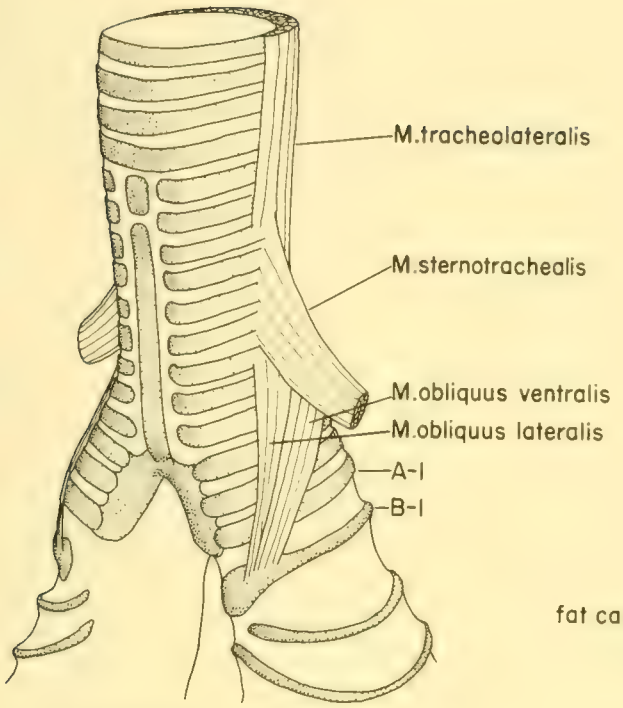
Tyrannidae (V), Dorsal

Colopteryx galeata, dorsolateral view, ×12.

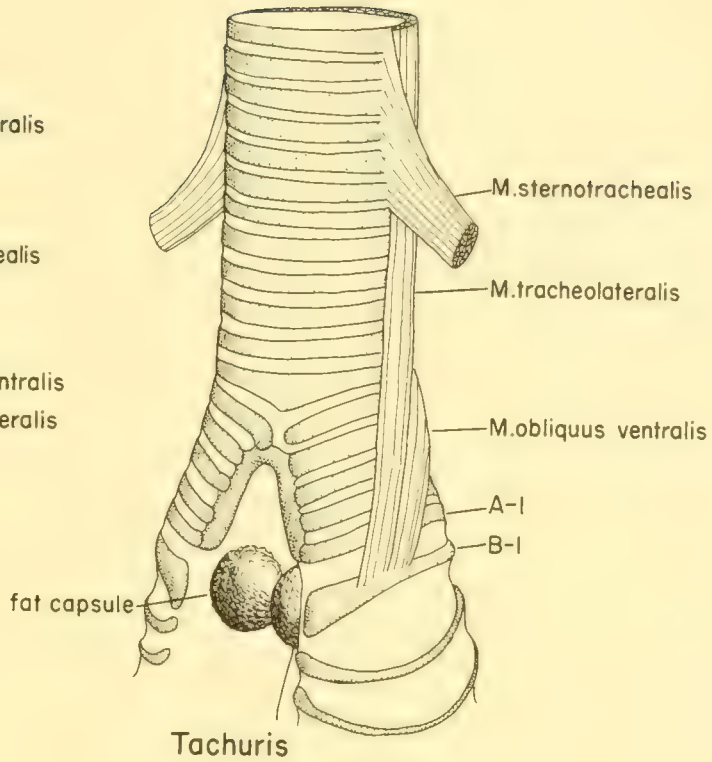
Tachuris rubrigastra, dorsolateral view, ×14.

Elaenia viridicata, dorsolateral view, ×8.

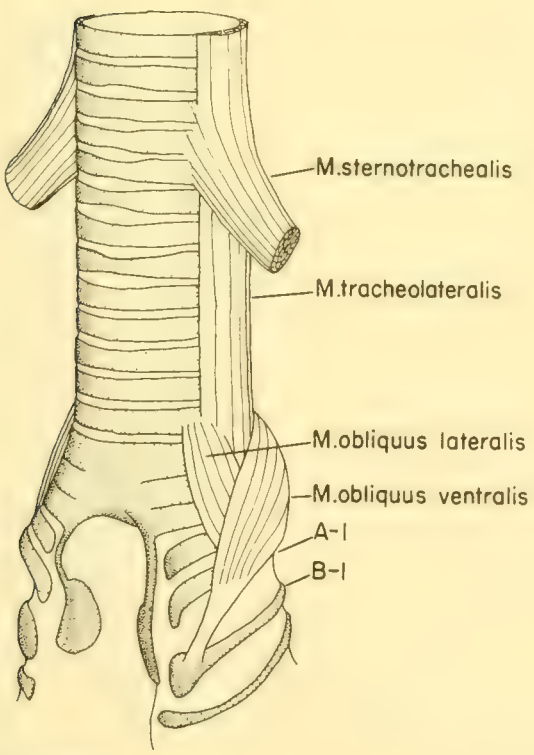
Pipromorpha oleaginea, dorsolateral view, ×9.



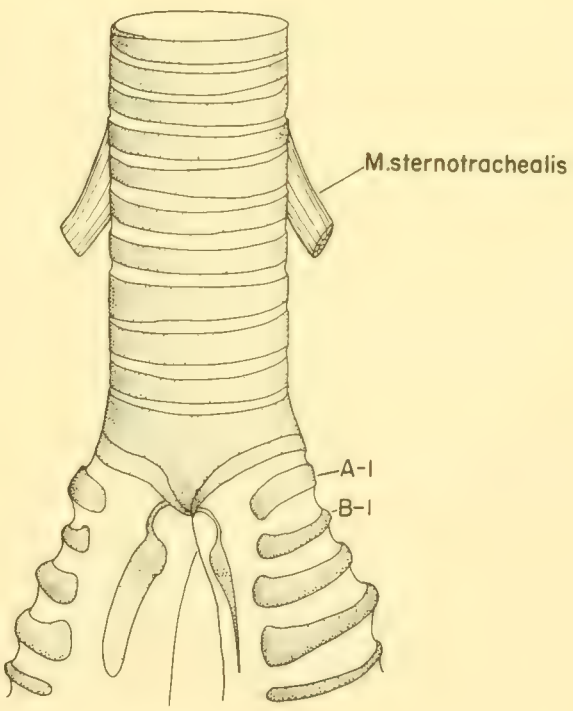
Colopteryx



Tachuris



Elaenia



Pipromorpha

PLATE 15

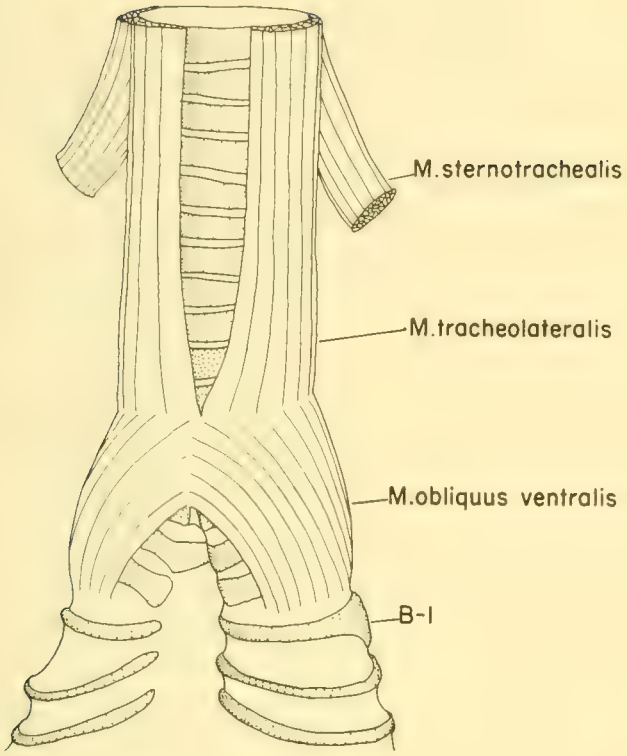
Cotingidae and Pipridae, Ventral

Attila spadiceus, ventrilateral view, ×6.

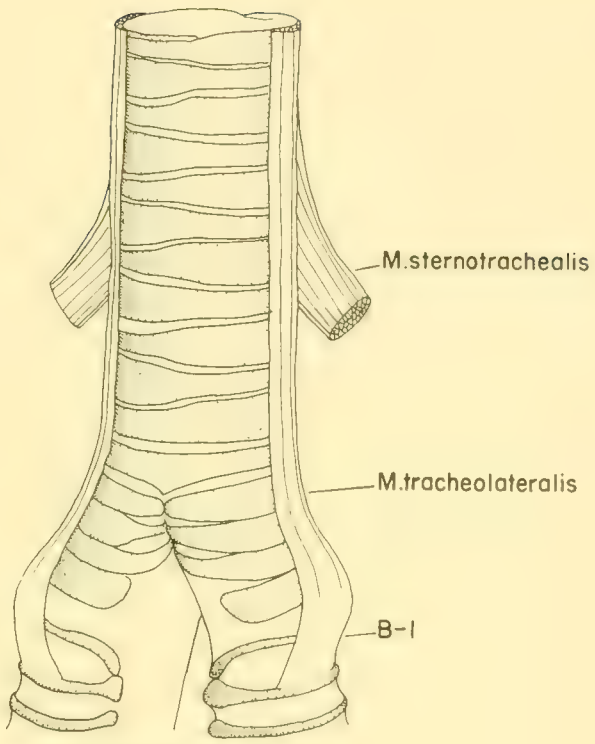
Cotinga amabilis, ventrilateral view, ×6.

Chiroxiphia lanceolata, ventrilateral view, ×8.

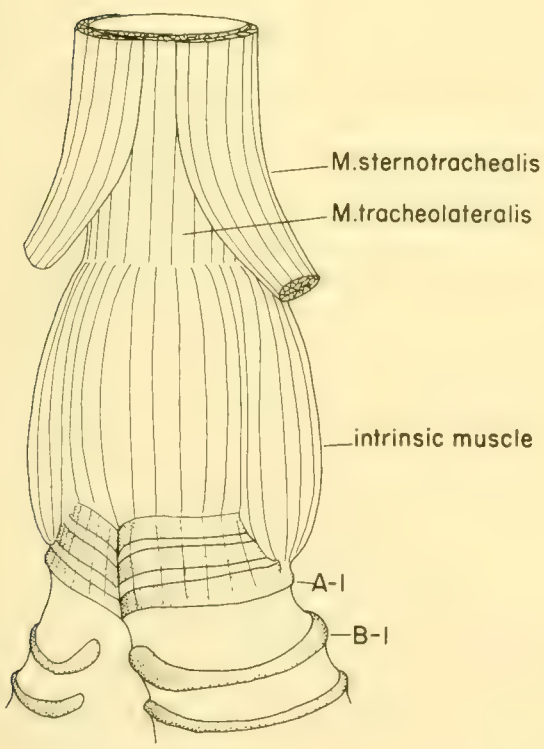
Corapipo leucorrhoa, ventrilateral view, ×9.



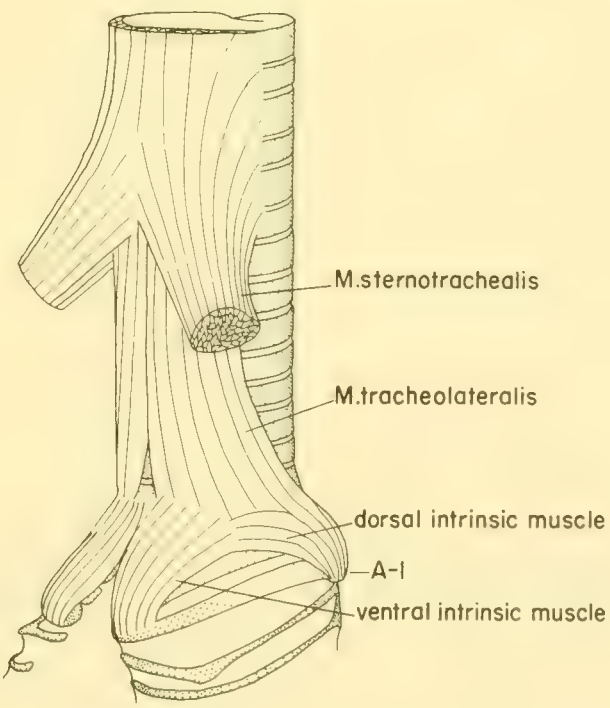
Attila



Cotinga



Chiroxiphia



Corapipo

PLATE 16

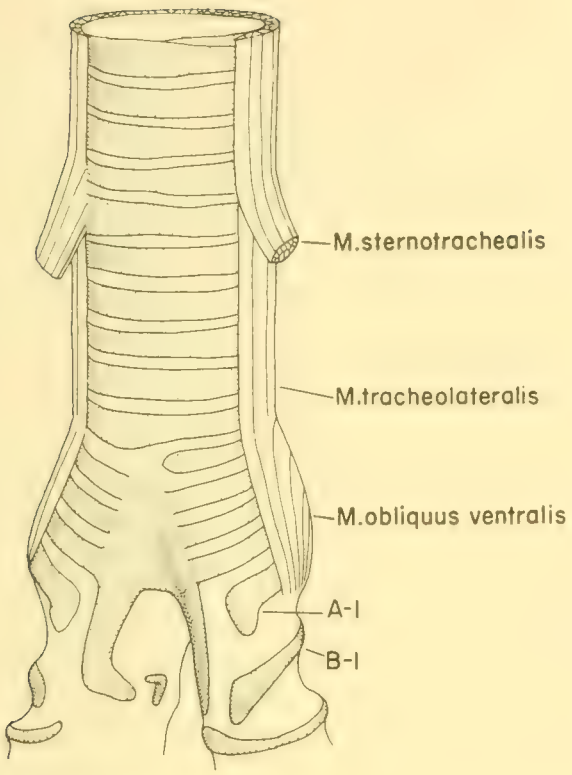
Cotingidae and Pipridae, Dorsal

Attila spadiceus, ventrilateral view, ×6.

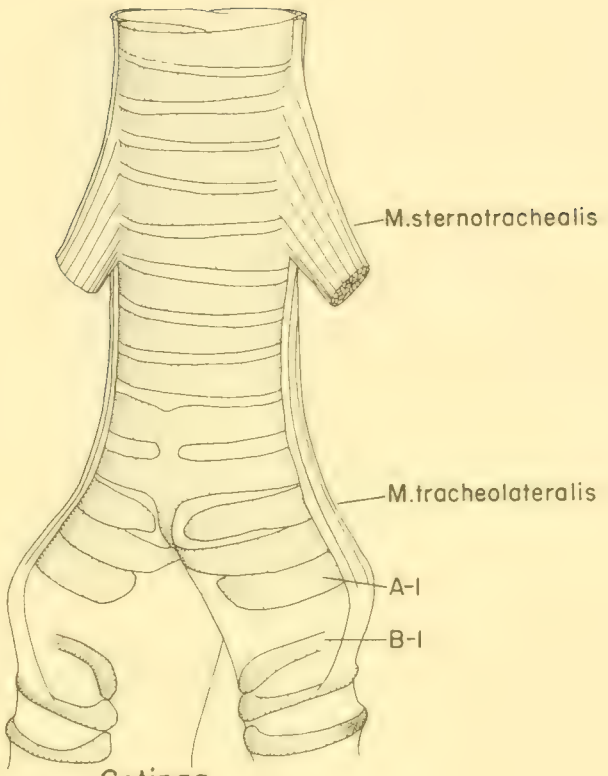
Cotinga amabilis, dorsolateral view, ×6.

Chiroxiphia lanceolata, dorsolateral view, ×8.

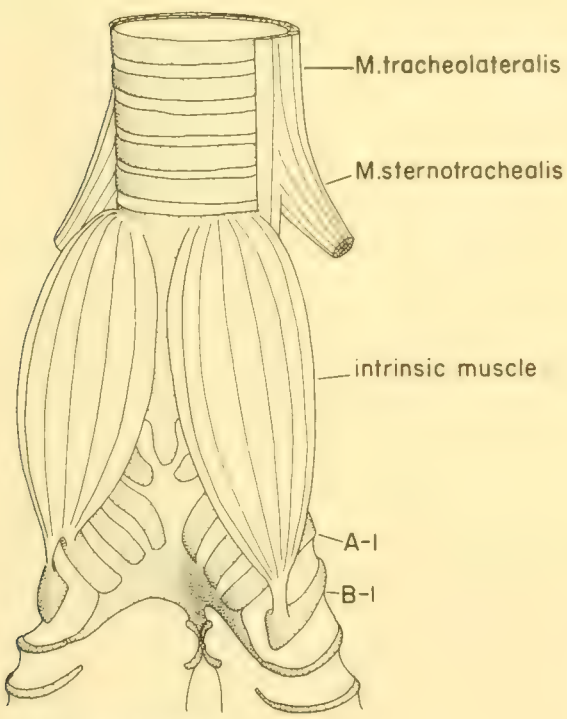
Corapipo leucorrhoa, dorsolateral view, ×9.



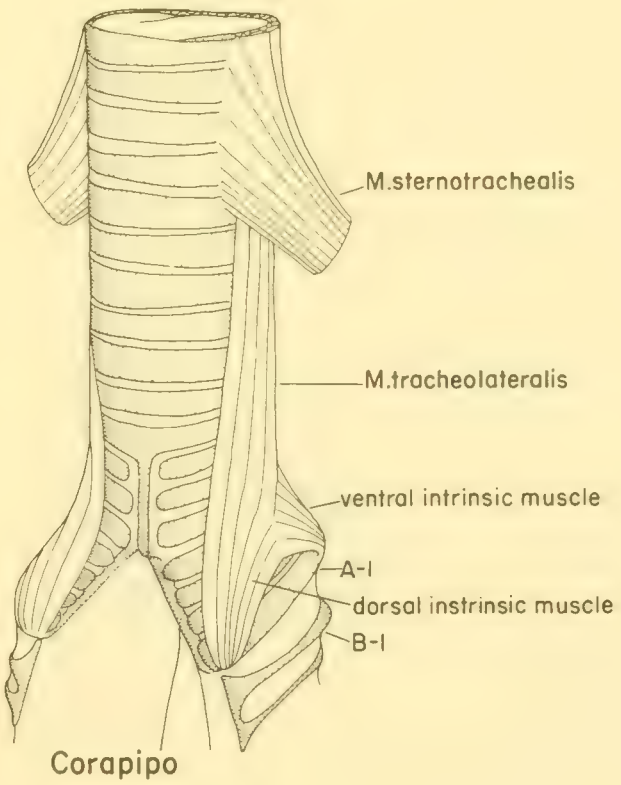
Attila



Cotinga



Chiroxiphia



Corapipo

PLATE 17

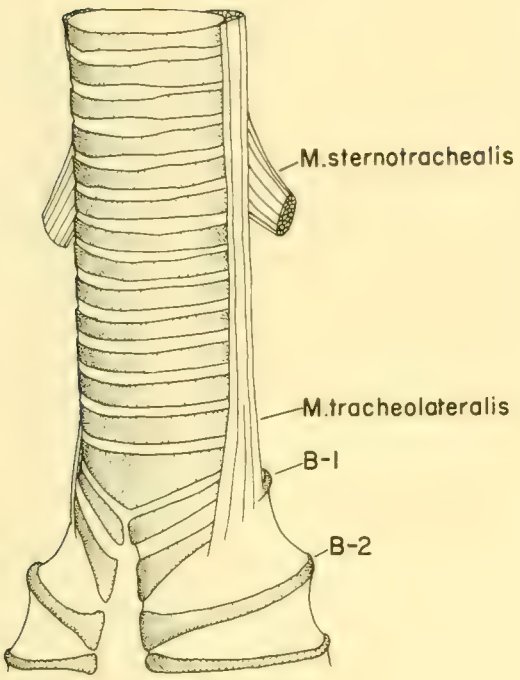
Miscellaneous Families, Ventral

Phytotoma rara, ventrilateral view, ×6.

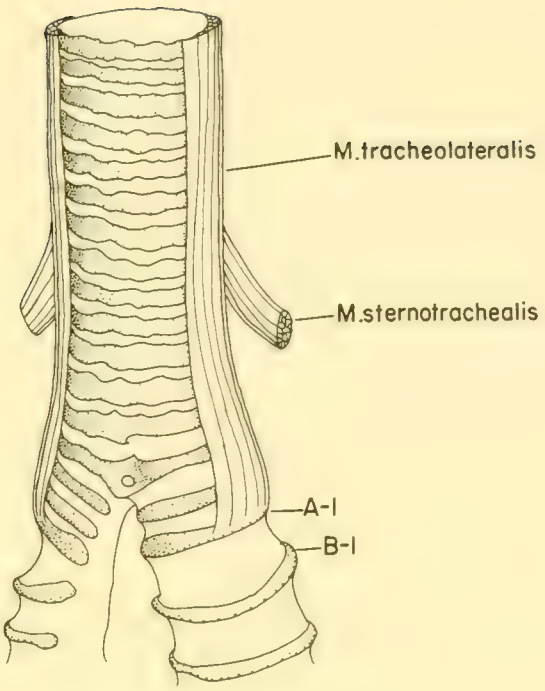
Pitta reichenowi, ventrilateral view, ×6.

Philepitta castanea, ventrilateral view, ×8.

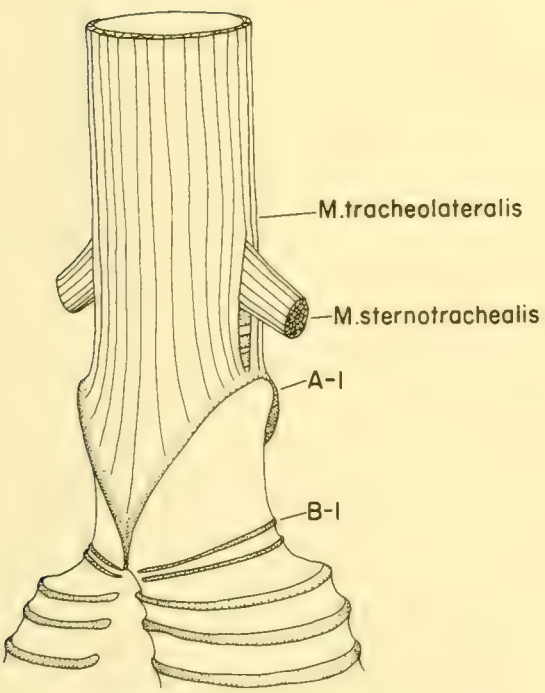
Menura novaehollandiae, ventrilateral view, ×5.



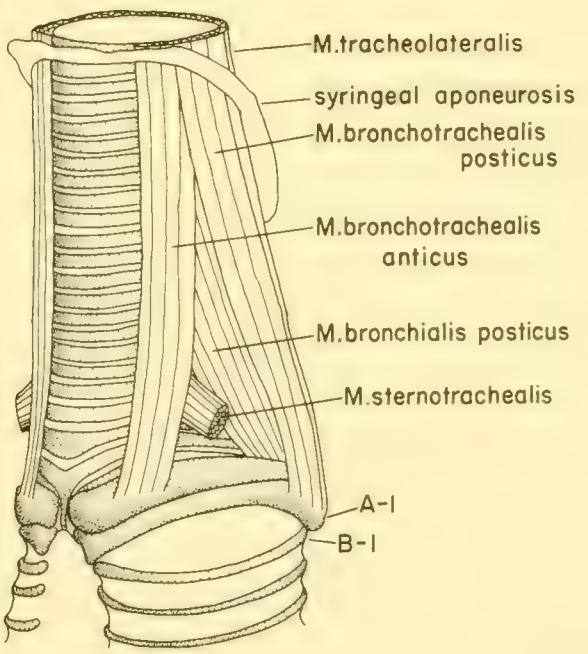
Phytotoma



Pitta



Philepitta



Menura

PLATE 18

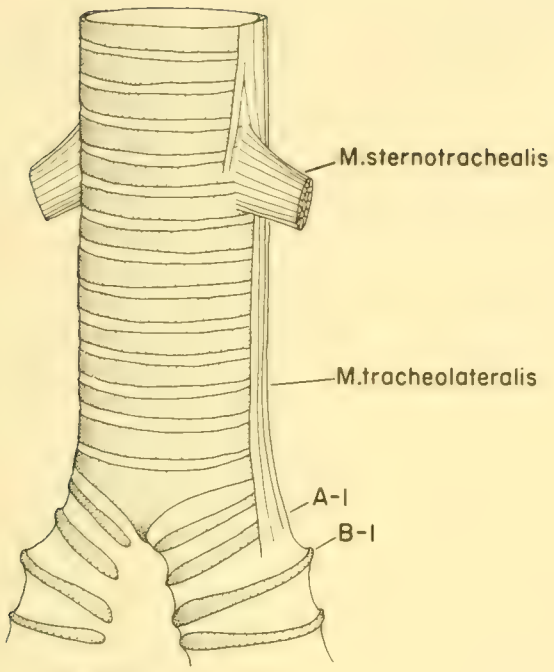
Miscellaneous Families, Dorsal

Phytotoma rara, ventrilateral view, ×6.

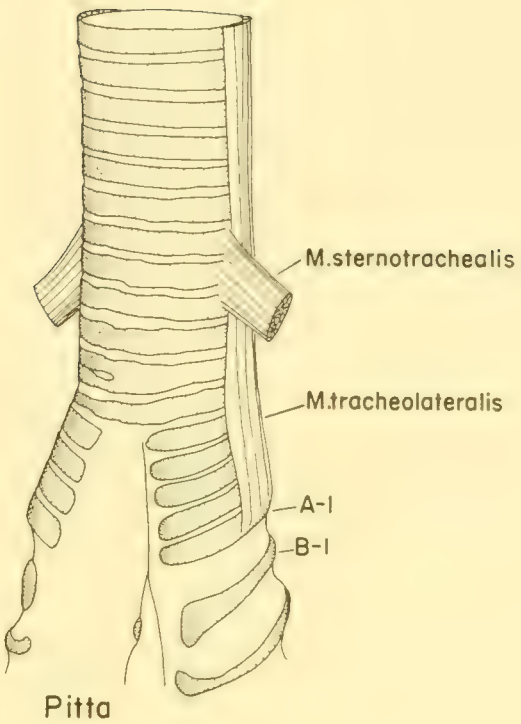
Pitta reichenowi, ventrilateral view, ×6.

Philepitta castanea, ventrilateral view, ×8.

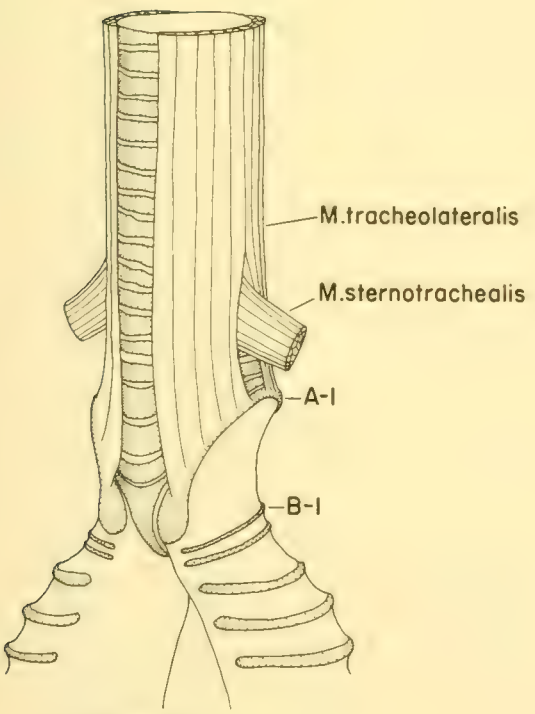
Menura novaehollandiae, ventrilateral view, ×5.



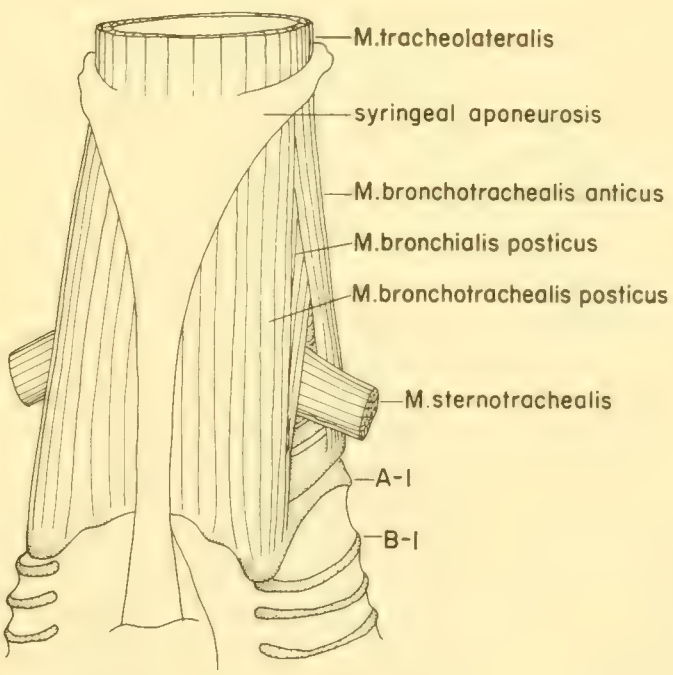
Phytotoma



Pitta



Philepitta



Menura

PLATE 19

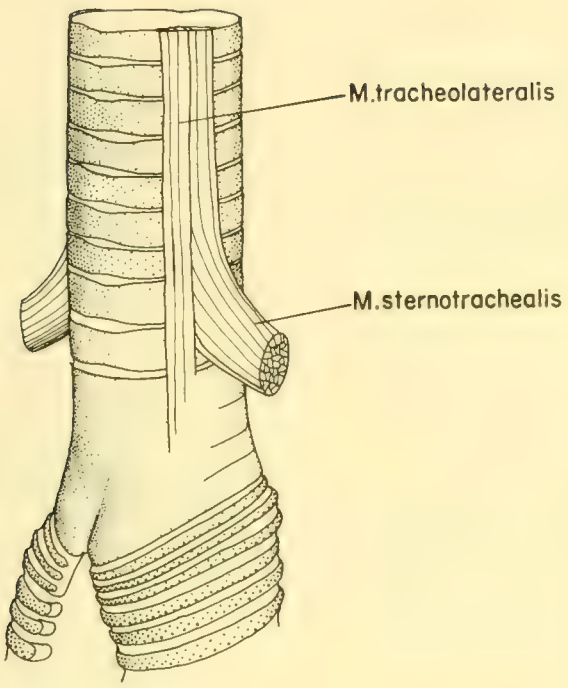
Acanthisittidae and Atrichornithidae

Acanthisitta chloris, ventrilateral view, ×9.

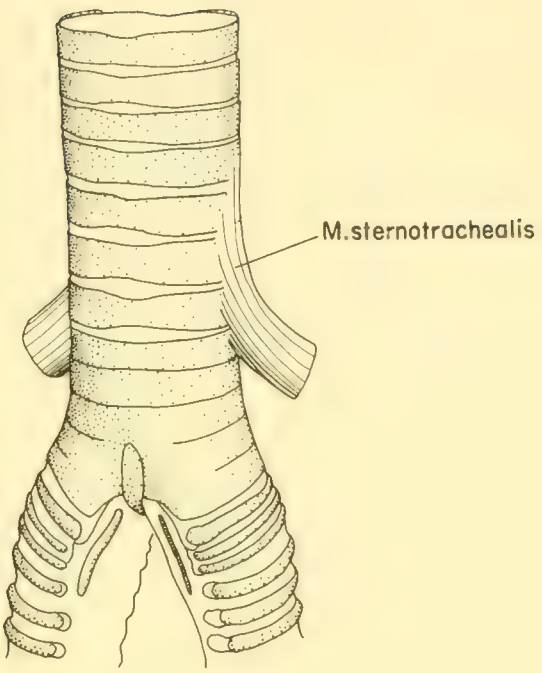
Same, dorsolateral view, ×9.

Atrichornis clamosus, ventrilateral view, ×6.

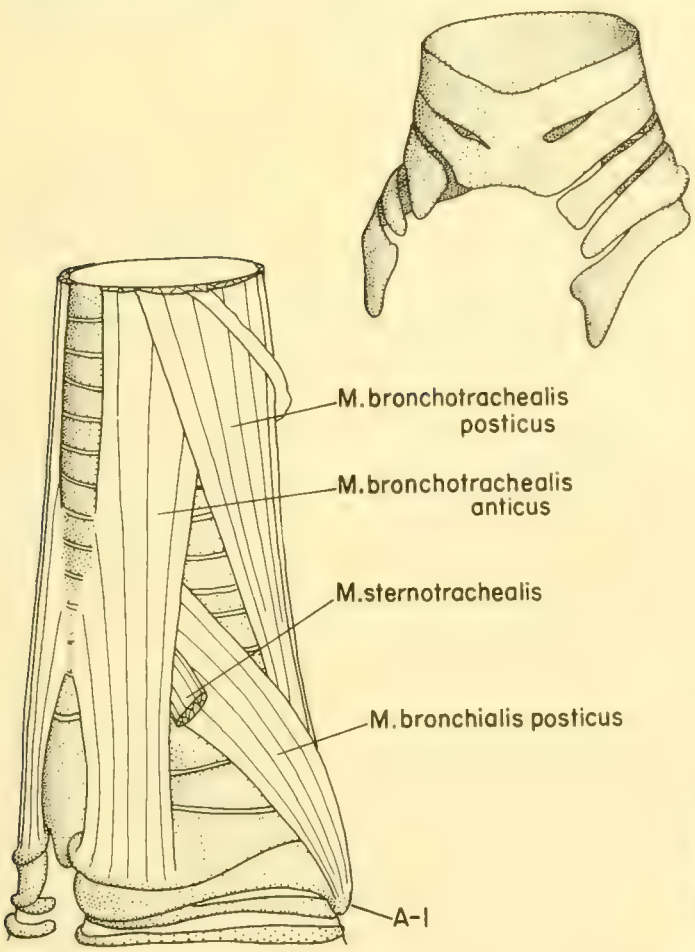
Same, dorsolateral view, ×6.



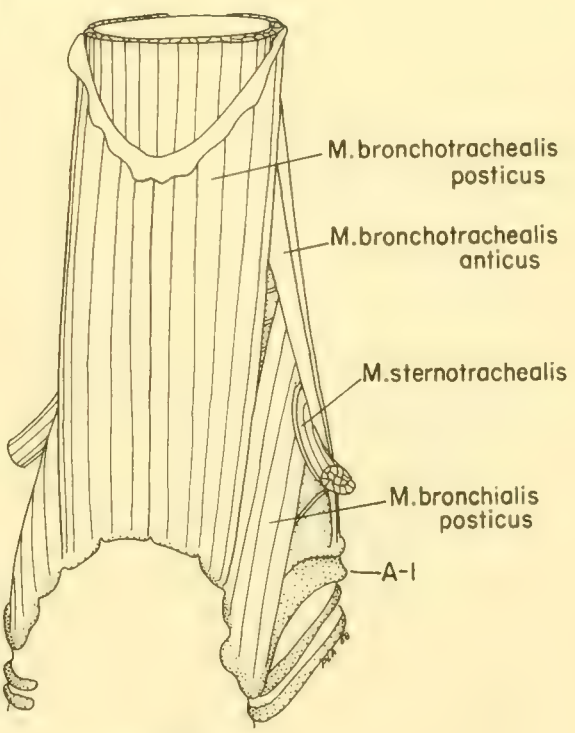
Acanthisitta, ventral



Acanthisitta, dorsal



Atrichornis, ventral



Atrichornis, dorsal

PLATE 20

Some Specializations of Lower A-Elements, Reading from Left to Right

Cephalopterus ornatus, A-5R and A-6, ventrilateral view, ×2.5.

Pyroderus scutatus, A-2R, A-2L and A-3, ventrilateral view, ×3.

Phytotoma rutila, A-1R and A-2, ventrilateral view, ×6.

Phytotoma rara, (YPM 2474), A-1R and A-2, ventrilateral view, ×6.

Tityra inquisitor, A-1R, A-2R, A-3, and A-4, ventrilateral view, ×3.

Onychorhynchus coronatus, A-3L and A-4, dorsolateral view, ×8.

Myiophobus fasciatus, A-4L and A-5R, dorsolateral view, ×8.

Heliochera rubrocristata, A-1R and A-2, ventrilateral view, ×3.

Machetornis rixosa, A-1L and A-2, dorsolateral view, ×6.

Capsiempis flaveola, A-1L and A-2 through A-5, dorsolateral view, ×6.

Phylloscartes ventralis, A-2R and A-3, ventrilateral view, ×8.

Mecocerculus leucophrys, A-1L and A-2 through A-4, dorsolateral view, ×6.

Tolmomyias sulphurescens, A-1L, A-2L, A-3L, A-4 and A-5, dorsolateral view, ×8.

Habrura pectoralis, YPM 2659, A-1L, A-2, A-3 and A-3aR, dorsolateral view, ×8.

Colorhamphus parvirostris, A-1L, A-2R and A-3, dorsolateral view, ×8.

Serpophaga subcristata, A-1L, and A-2 through A-5, and left internal cartilage, dorsolateral view, ×8.

Euscarthmus melorhyphus, A-2L and A-3 through A-9, dorsolateral view, ×8.

Pogonotriccus eximius, A-1L, A-2L, A-3 and A-4, dorsolateral view, ×8.

Phaeomyias murina, YPM 2046, A-1L and A-2R through A-4, dorsolateral view, ×8.

Phaeomyias murina, YPM 2038, A-1L, A-2 and A-3, dorsolateral view, ×8.

Stigmatura budytoides, A-1L through A-8 and internal cartilages, dorsolateral view, ×9.

Elaenia caniceps, A-1L, A-2 through A-4, dorsolateral view, ×8.

Neodrepanis coruscans, A-1L and internal cartilages, dorsolateral view, ×9.

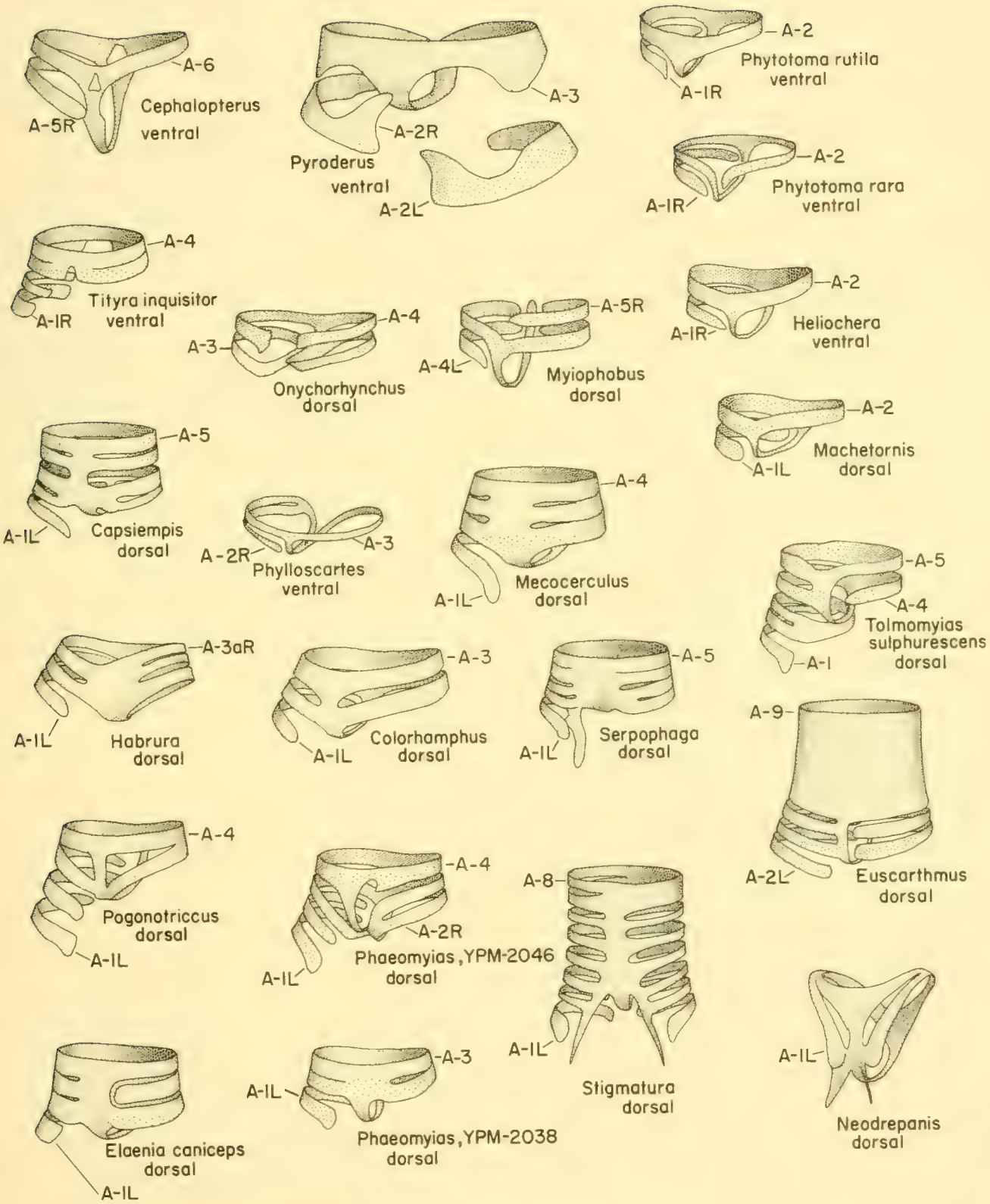

A-6
A-5R
Cephalopterus
ventral
A-3
A-2R
Pyroderus
ventral
A-2L
A-2
A-1R
Phytotoma rutila
ventral
A-2
A-1R
Phytotoma rara
ventral
A-4
A-1R
Tityra inquisitor
ventral
A-4
A-3
Onychorhynchus
dorsal
A-5R
A-4L
Myiophobus
dorsal
A-2
A-1R
Heliochera
ventral
A-2
A-1L
Machetornis
dorsal
A-5
A-1L
Capsiempis
dorsal
A-3
A-2R
Phylloscartes
ventral
A-4
A-1L
Mecocerculus
dorsal
A-5
A-4
A-1
Tolmomyias
sulphurescens
dorsal
A-3aR
A-1L
Habrura
dorsal
A-3
A-1L
Colorhamphus
dorsal
A-5
A-1L
Serpophaga
dorsal
A-9
A-2L
Euscarthmus
dorsal
A-4
A-1L
Pogonotriccus
dorsal
A-4
A-2R
A-1L
Phaeomyias, YPM-2046
dorsal
A-8
A-1L
Stigmatura
dorsal
A-1L
Neodrepanis
dorsal
A-1L
Elaenia caniceps
dorsal
A-3
A-1L
Phaeomyias, YPM-2038
dorsal

PLATE 21

The Oscine Syrinx

(Reprinted, by permission, from A. J. Berger and J.C. George, *Avian Myology,* in which this drawing originally appeared. © 1966 by Academic Press, Inc.)

FIG. 1 *Corvus brachyrhynchus*, ventrilateral view, ×5.

FIG. 2 Same, dorsolateral view, ×5.

FIG. 3 Same, A-1, A-3 and drum, left dorsolateral view, ×3.

FIG. 4 Same, A-3 and drum, left ventrilateral view, ×5.

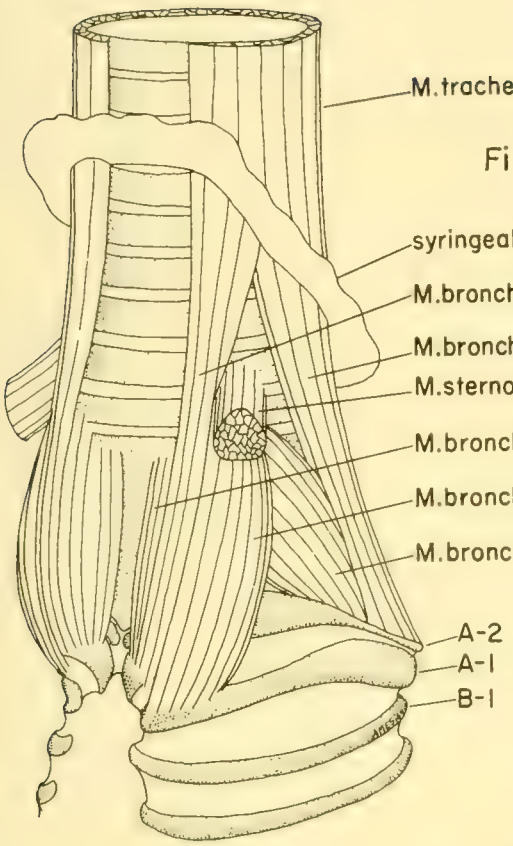


Fig.1

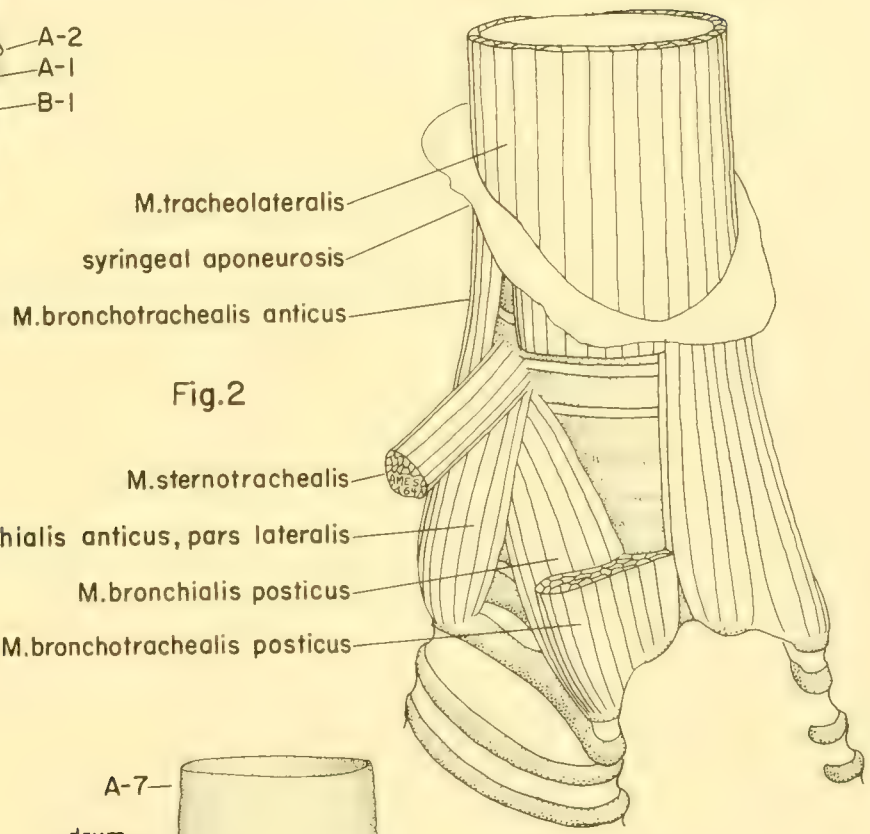


Fig.2

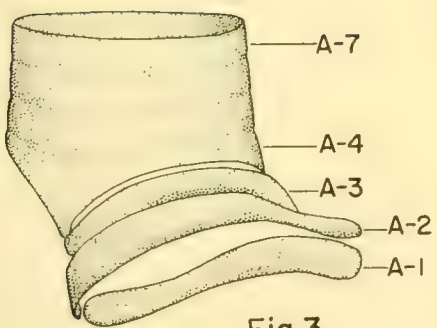


Fig.3

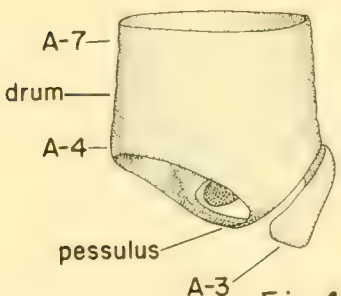


Fig.4

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